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JOURNAL OF
MARINE RESEARCH

VOLUME IX 1950 NUMBER 1

NOTES ON SIPHONOPHORES

1. Siphonophores from the Marshall Islands

By

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ABSTRACT

The Crossroads plankton collection extends the range of about 30 siphonophores to the Marshall Islands, but only one third of these was taken in the lagoons. Of the species recorded, *Galetta bigelowi* is new, *Lensia grimaldii* was taken in the Pacific for the first time, and *Diphyes chamissonis*, which is restricted to the Indo-Pacific region, was taken in quantity in Rongelap Lagoon, as it had been in the Great Barrier Reef Lagoon. The significance of this habitat in limiting the distribution of *D. chamissonis* is not apparent.

The siphonophores formed a small fraction of the zooplankton in the area. Comparison with rough estimates of the population of the Mediterranean and of the Great Barrier Reef Lagoon suggests that this sparsity is not uncommon. On the other hand, some evidence of swarming is afforded.

Galetta bigelowi n. sp. is described and figured.

Introduction. During the spring and summer of 1946 some plankton collections were made in the Marshall Islands area as part of the oceanographic program for Operation CROSSROADS[2] (Barnes,

[1] Contribution No. 481 from the Woods Hole Oceanographic Institution.

[2] For convenience, the tests at Bikini in 1946 under the joint auspices of the U. S. Army and Navy, which included an oceanographic survey in the Marshall Islands area during the spring and summer months, is referred to as Operation CROSSROADS. Observations were taken in the vicinity of Eniwetok, Rongelap, and Rongerik atolls, as well as in the vicinity of Bikini Atoll.

Bumpus, and Lyman, 1948; Ford, 1949; Johnson, 1949; LaFond, 1949; Sargent and Austin, 1949; von Arx, 1948). I am indebted to Dr. Martin W. Johnson of the Scripps Institution of Oceanography for the opportunity to examine the siphonophores in the material he collected.

Insofar as I can ascertain, this is the first published record of any extensive or systematic collection of siphonophores from this particular area. Agassiz and Mayer (1902: 166) mention having drawn a specimen of *Abylopsis tetragona* (as *Abyla huxleyi* Haeckel) that was "obtained near Rongelap Atoll, Marshall Islands," but Agassiz made no regular plankton hauls after leaving the Society Islands (Agassiz and Mayer, 1902: 139, pl. 14). The CARNEGIE, on her last cruise, passed somewhat to the east and north of the Marshall Islands. From the plankton taken along that portion of her route, Totton lists a number of the new species which he described recently (Totton, 1941), but as yet he has not published a complete enumeration of the species from that region. The SHINTOKU MARU (Schott, 1935), on return voyages from Australia to Japan in the early 1930's, passed to the south and west of the Marshall Islands, but I have been unable to locate a report on siphonophores resulting from these traverses.

Geographical Considerations. The CROSSROADS collection is interesting in that it extends the range of about 30 siphonophore species to this area (Table I). However, inasmuch as the collection of siphonophores was incidental to other work, it is improbable that an adequate census of this group was made, since many species are now known to live in some numbers at considerable depths[3] (Bigelow and Sears, 1937). In this connection, it is noteworthy that only about one-third of the species recorded were actually taken within the shallower waters of the lagoons, despite the fact that four times as many tows were made there as in the waters outside the atolls (Table I). This suggests that many of the species taken outside were "strays" from greater depths, especially as they were not taken regularly (Table I) or in any quantity. On the other hand, of the five species prevalent (but seldom numerous) in the lagoons, four (*Abylopsis eschscholtzii* Huxley, *Bassia bassensis* Quoy and Gaimard, *Diphyes chamissonis* Huxley, and *Lensia subtilis* Chun) have previously been known to inhabit the warmer surface waters (Leloup and Hentschel, 1935; Russell and Colman, 1935; Bigelow and Sears, 1937). Although the fifth (*Chelophyes contorta* Lens and Van Riemsdijk) is still rela-

[3] Only the surface layers down to about 60 meters were sampled by using a plankton sampler (Clarke and Bumpus, 1940) or small nets, 10 in., and 30, 40 and 70 cm. in diameter, made of No. 2, 8, 10 or 20 bolting silk (Johnson, personal communication).

TABLE I. Number of Stations (with Approximate Locality) Where Various Species of Siphonophores Were Taken During Operation CROSSROADS

Species	*Bikini Atoll*		*Rongelap Atoll*	*Rongerik Atoll*		*Eniwetok Atoll*		*Destroyer hauls between 2° 15′ S. & 9° 00′ N. and 166° 39′ E. and 168° E.*
	Inside lagoon	*Outside lagoon*	*Inside lagoon*	*Inside lagoon*	*Outside lagoon*	*Inside lagoon*	*Outside lagoon*	
Abyla leuckartii	—	1	—	—	—	—	—	—
Abyla trigona	—	3	—	—	1	—	—	—
Abylopsis eschscholtzii	10+1?*	47+1?	11	2	1	—	1	5
Abylopsis tetragona	—	18	2	—	—	—	1	1
Agalma okeni	1?	6+1?	—	—	1	—	1	2
Agalmid	4+1?	2	2	—	—	—	—	1
Bassia bassensis	19	42+1?	11	3	1	—	1	2
Chelophyes appendiculata	—	7	1	—	1	—	—	—
Chelophyes contorta	33+1?	40+1?	21	3	1	1	2	2
Dimophyes arctica	—	4	—	—	—	—	—	—
Diphyes bojani	3	20	5+1?	2	1	—	—	3
Diphyes chamissonis	15+19?	22+16?	42	2+2?	1	2?	—	5+2?
Diphyes dispar	3	20	2	—	—	—	1	6
Enneagonum hyalinum	—	1?	—	—	—	—	—	—
Eudoxoides mitra	—	6+3?	—	—	—	—	—	—
Eudoxoides spiralis	—	1	1	—	—	—	—	—
Galetta australis	—	6+1?	—	—	—	—	—	1
Galetta chuni	1	2+3?	2	—	—	—	—	1
Galetta bigelowi	—	2	—	—	1	—	—	—
Lensia campanella	—	6	—	—	1	—	—	—
Lensia conoidea	4+3?	6+5?	3+3?	—	—	—	1?	1+1?
Lensia cossack	—	4+2?	—	—	1	—	—	—
Lensia fowleri	—	2	—	—	—	—	—	—
Lensia grimaldii	—	1	—	—	—	—	—	—
Lensia hotspur	—	—	—	—	1	—	—	—
Lensia multicristata	—	2+2?	—	—	—	—	—	—
Lensia subtilis	10	14+1?	4	1	1	—	—	4
Lensia subtiloides	—	6	—	—	1	—	—	—
Lensia sp.?	—	4	—	—	—	—	1	—
Rosacea plicata	—	1	—	—	—	—	—	—
Sulculeolaria monoica	—	3	—	—	—	—	—	—
Sulculeolaria quadridentata	—	1	—	—	—	—	—	—
No. of stations where siphonophores were taken	54	58	42	6	1	2	2	11
No. of stations where plankton tows were taken	210	74	80	19	1	27	3	?

* Since the preservation of the siphonophores was not always sufficiently good to identify positively the various species, a question mark in the above table indicates some uncertainty in identification.

tively unfamiliar, preliminary examination of several DANA stations in the Pacific suggests that this species will also prove to be an inhabitant of the warmer superficial layers.

Of these five species, *Diphyes chamissonis* is unique in that it is the only siphonophore restricted to the Indo-Pacific region. Thus, judging from earlier accounts, it is scarce in the Indian Ocean (Browne, 1926); it is fairly common in the Malay Archipelago (Lens and Van Riemsdijk, 1908), in the Philippines (Bigelow, 1919) and off the east coast of Australia (Huxley, 1858; Russell and Colman, 1935), where it may be the most common and most abundant siphonophore (Table II); it has been recorded to the north (Bigelow, 1913; Kawamura, 1915) but not from the eastern Pacific (Bigelow, 1911). While the present records thus extend eastward the area outlined above, they do not delimit its chief centers of abundance.

Perhaps it is more than a coincidence that the only two reports of *Diphyes chamissonis* in any great quantities are from lagoons, i. e., Rongelap lagoon and the Great Barrier Reef lagoon where it was also the most prevalent of the siphonophores and the second most abundant (Russell and Colman, 1935: 262). However, factors which may limit the distribution or abundance of this or any other siphonophore species in other areas, such as salinity, temperature, currents, and bottom topography (Russell and Colman, 1935; Leloup and Hentschel, 1935; Bigelow and Sears, 1937), are not apparent in analyzing the distribution of the various species in this area; this may be due in part to the small number of individuals taken in any particular tow and possibly because the collection was made over such a short period of time. Thus it will be necessary to await the analysis of other collections before we can determine whether *Diphyes chamissonis* is restricted to the Indo-Pacific because it propagates chiefly in shallow lagoon waters, or whether its dispersal to other areas is limited by temperature, currents, or some other factor.

Of the other species (Table I), none of which was taken in quantity in the Marshall Islands area, four species[4] are among the most common and most numerous in collections made in all oceans; 17 species[5] are

[4] *Abylopsis eschscholtzii* Huxley, *A. tetragona* Otto, *Bassia bassensis* Quoy and Gaimard, and *Chelophyes appendiculata* Eschscholtz.

[5] *Abyla leuckartii* Huxley, *A. trigona* Quoy and Gaimard, *Agalma okeni* Eschscholtz, *Chelophyes contorta* Lens and Van Riemsdijk, *Dimophyes arctica* Chun, *Diphyes bojani* Chun, *D. dispar* Chamisso and Eysenhardt, *Enneagonum hyalinum* Quoy and Gaimard, *Eudoxoides mitra* Huxley, *E. spiralis*, Bigelow, *Galetta australis* Quoy and Gaimard, *G. chuni* Lens and Van Riemsdijk, *Lensia subtilis* Chun, *L. subtiloides* Lens and Van Riemsdijk, *Rosacea plicata* Quoy and Gaimard, *Sulculeolaria monoica* Chun, and *S. quadridentata* Quoy and Gaimard.

TABLE II. Dominant Siphonophores in Various Pacific Ocean Areas

Locality	*Species*	*Remarks*
Marquesas Islands	*Diphyes dispar* Chamisso & Eysenhardt (as *Diphyopsis angustata* and *Ersaea angustata*)	"In the tropical regions of the Pacific—commonest of all Siphonophorae" (Agassiz & Mayer, 1902: 162).
	Chelophyes appendiculata Eschscholtz (as *Diphyopsis appendiculata* and *Ersaea appendiculata*)	"Abundant throughout tropical regions of Pacific" (Agassiz & Mayer, 1902: 160).
Fiji Islands	*Diphyes dispar* Chamisso & Eysenhardt (as *Diphyopsis angustata*)	"Common among the Fiji Islands" (Agassiz & Mayer, 1899: 180).
Eastern Tropical Pacific	*Abylopsis tetragona* Otto *Bassia bassensis* Quoy & Gaimard *Chelophyes appendiculata* Eschscholtz (as *Diphyes appendiculata*) *Diphyes bojani* Chun *Eudoxoides mitra* Huxley (as *Diphyopsis mitra*)	"Five of the commoner" species (Bigelow, 1911: 358).
Great Barrier Reef	*Diphyes chamissonis* Huxley *Lensia subtiloides* Lens & Van Riemsdijk	"Only really abundant sipnonophores in the barrier reef lagoon" (Russell & Colman, 1935: 256).
Bass Straits	*Chelophyes appendiculata* Eschscholtz (as *Diphyes appendiculata*)	"Particularly abundant" (Huxley, 1858: 35).
	Bassia bassensis Quoy & Gaimard (as *Sphenoides australis*)	"Abounded" (Huxley, 1858: 62).
South of Tasmania	*Bassia bassensis* Quoy & Gaimard (as *Abyla bassensis*)	"Great abundance" (Huxley, 1858: 46).
East coast of Australia and in Louisiade Archipelago	*Diphyes chamissonis* Huxley	"Took . . . repeatedly" (Huxley, 1858: 36).
Philippines	*Diphyes chamissonis* Huxley	67 superior nectophores;
	Diphyes dispar Chamisso & Eysenhardt	149 nectophores;
	Galetta australis Quoy & Gaimard (as *Galeolaria australis*)	282 nectophores;
	Abylopsis tetragona Otto	87 colonies. (Bigelow, 1919).
Northwest Pacific	*Galetta australis* Quoy & Gaimard (as *Galeolaria australis*)	111 superior nectophores;
	Dimophyes arctica Chun (as *Diphyes arctica*)	74 superior nectophores. (Bigelow, 1913).
Malay Archipelago	*Abylopsis tetragona* Otto (as *Abyla pentagona* and *Aglaisma cuboides*)	169 colonies (or parts thereof), 30 stations;
	Abylopsis eschscholtzii Huxley (as *Abyla quincunx* and *Aglaismoides eschscholtzii*)	138 colonies (or parts thereof), 28 stations;
	Chelophyes contorta Lens & Van Riemsdijk (as *Diphyes contorta*)	296 specimens, 36 stations;
	Diphyes chamissonis Huxley (as *Diphyopsis weberi*)	272 specimens, 20 stations. (Lens & Van Riemsdijk, 1908).

nearly as widespread, but less numerous; three species[6] are found rather more regularly and in greater abundance wherever the deeper layers have been sampled; and three small species,[7] all described within the past 25 years, will probably prove to be widespread.[8] [9]

The only species apparently reported for the first time from the Pacific are *Lensia grimaldii* Leloup, originally described from the vicinity of the Azores (Leloup, 1933) and *Galetta bigelowi* n. sp. (see description on p. 10).

Abundance. Only one species, *Diphyes chamissonis*, occurred in sufficient quantity in the tows to warrant comparison with the general abundance of other plankton constituents in the Marshall Island area and with the numbers of siphonophores in other seas. Actually, an active center of reproduction in Rongelap lagoon at the time of the mid-June survey (Table III) appears to have been responsible for the

TABLE III. Abundance of *Diphyes chamissonis* in Various Parts of the Marshall Islands. Most Tows Were Roughly of Twenty Minute Duration Except Those from the Destroyer Which Averaged One Hour. Numbers Are Unadjusted for Type of Net or Duration of Haul

	Colonies		*Eudoxids*		*No. of tows taking D. chamissonis.*	
	Av.	*Max.*	*Av.*	*Max.*	*All types of gear*	*Clarke-Bumpus Sampler*
Bikini Atoll						
Inside	1	1	2	15	34	28
Outside	1	1	3	12	38	32
Rongelap Atoll						
Inside	82	527	114	842	42	28
Rongerik Atoll						
Inside	0	0	3	5	4	2
Outside	0	0	21	21	1	0
Eniwetok Atoll						
Inside	0	0	2	3	2	2
Destroyer haul	1	1	7	33	7	0

abundance of *D. chamissonis*, since both nectophores and free eudoxids were taken there ranging from a few millimeters to nearly a centimeter.

At one station in the central portion of Bikini lagoon, Johnson (1949: 240, fig. 8) found an average of 66 copepods per cubic meter of water and as many as 255 specimens of *Undinula vulgaris*, the most

[6] *Lensia conoidea* Keferstein and Ehlers, *L. fowleri* Bigelow, and *L. multicristata* Moser.

[7] *L. campanella* Moser, *L. grimaldii* Leloup, and *L. hotspur* Totton.

[8] Totton (personal communication) has found them in some numbers in the Discovery material, while I have found them among the Dana siphonophores from the Pacific.

[9] See Bigelow and Sears (1937) for a discussion of this, as well as for references to earlier work.

abundant copepod. In contrast, not more than one specimen of either generation of *D. chamissonis* per cubic meter of water was taken at any one station there. Furthermore, this species was present in only 16% of the tows in that lagoon. Even the richest tow of *D. chamissonis*, made with a Clarke-Bumpus sampler in Rongelap lagoon, yielded only half as many specimens (29 eudoxids per cubic meter of water) as the *average* copepod catch and only about one-tenth as many as the *biggest* catch of *Undinula vulgaris* in Bikini lagoon, supposing such a comparison to be permissible. At best, then, siphonophores formed only a very small fraction of the total larger zooplankton[10] population at the time of the CROSSROADS survey.

In short, we must come to the conclusion that, insofar as we may estimate the general abundance of siphonophores, they are distinctly scarce when compared with other constituents of the plankton, particularly in an area (Marshall Islands) where the plankton as a whole is definitely scarce (Johnson, 1949: 239). Furthermore, this situation appears to be similar to that in the Great Barrier Reef lagoon (Russell and Colman, 1935: 254) where the siphonophores (taken in the coarse silk net) proved to be 0.3 to 4.8% of the total number of animals caught. It is to be suspected that future examination of more or less quantitative hauls of the plankton as a whole from elsewhere will further substantiate this conclusion. There is a suggestion of this in the catches made with stramin nets[11] in the Mediterranean and adjacent parts of the Atlantic, where a rough total of 264,920 euphausids (Ruud, 1936: List of Material), 40,000 hyperiid amphipods (Stephensen, 1925: 227), and 95,000 siphonophores (Bigelow and Sears, 1937: 3) were taken by the THOR. No figure can be given for the other groups, the figures not being readily obtainable from the published reports, or for the copepods, for which a report is lacking.

Unfortunately, since no indication is given of the speed of towing or the volume of water strained when samples were taken in the Great Barrier Reef lagoon (Russell and Colman, 1931), it is impossible to compute the numbers per cubic meter of water for comparison with the figures obtained in the Marshall Island area. Thus, the only previous report expressing the abundance of siphonophores in terms

[10] The unicellular zooplankton discussed in Johnson's (1949) paper has not been considered in this connection, since these forms are not generally taken in the same nets used in capturing siphonophores.

[11] Catches made with stramin nets contain proportionately higher numbers of siphonophores than those taken with silk nets (Russell and Colman, 1935), presumably because many of the smaller copepods slip through the relatively large meshes.

which can be made at all comparable to those taken on Operation CROSSROADS is the one based on the THOR collection (Bigelow and Sears, 1937). It is questionable, of course, whether one is justified in comparing catches taken with Petersen's Young-Fish Trawl, the net used chiefly in making the THOR tows, with those taken by the Clarke-Bumpus Plankton Samplers, used on Operation CROSSROADS. Admittedly the estimates for the abundance of the THOR siphonophores were rough approximations (Bigelow and Sears, 1937: 68–69), while the volume of water flowing through the sampler is known and hence the number of organisms in a given body of water can be calculated rather accurately. Despite the great difference in nets, it is interesting to note, at least in the absence of more comparable data, that the richest haul of any single species (*Diphyes chamissonis*) in Rongelap lagoon was apparently about five times as great as the richest taken by the THOR (*Bassia bassensis*) in the Atlantic (Table IV). This is quite astonishing in view of the fact that the lagoon

TABLE IV. COMPARISON OF MAXIMAL CATCHES IN THE MARSHALL ISLANDS AND IN THE ATLANTIC

	Marshall Islands Diphyes chamissonis (eudoxids)		*Atlantic Bassia bassensis (colonies)*
	Clarke-Bumpus‡ sampler, No. 2 silk	*40 cm. net, No. 8 silk*	*Young-Fish Trawl*
Actual catch	411	842	—
No. specimens per m^3 water	29	32*	6†
Volume (m^3) of water per specimen	.03	.03	.18

‡ Dr. Johnson (personal communication) informs me that the sampler actually strained 10,667 liters of water.

* Based on the assumptions (1) that No. 8 bolting silk will filter about three quarters of the amount of No. 2 silk (from comparisons with plankton samplers) and (2) that the amount filtered is increased in direct proportion to the area of the net opening (about 240 cm^2 for the plankton sampler; 1,257 cm^2 for the 40 cm. net).

† The most abundant catch of a single species of siphonophores taken by the THOR (Bigelow and Sears, 1937: 139).

waters in the Marshalls were seemingly not an especially favorable environment for siphonophores, as mentioned above (see Table I); however, perhaps it lends support to the idea that this particular species is indigenous to shallow lagoon waters, as suggested previously.

It is a generally recognized fact that plankton organisms are not regularly dispersed in a given body of water but occur in more or less dense swarms. Patches of plankton organisms are observed frequently at the sea surface in such density that they discolor the water, i. e.,

"red water" (dinoflagellates),[12] "red feed" (*Calanus finmarchicus*[13] or various euphausids), or swarms of Cyanea which occasionally form a thick "soup" off the New England Coast. In contrast to these dense masses, Stephensen (1925: 234) speaks of "shoals" of amphipods, when more than 100 specimens of a species were taken in a 30 minute tow (i. e., about 1 specimen per 3 cubic meters of water).

Other than the marked differences in the numbers caught from station to station, no evidence for the patchiness of siphonophores has been described previously. This is chiefly due to the fact that the older tow nets with their wide mouths, hauled long distances through the water, strained so much water that the catch represented the average rather than the actual condition prevailing over a considerable area—perhaps several miles. The rather limited amount of water strained through the small opening of a plankton sampler apparently affords a means of ascertaining more accurately the actual density of rather small patches and conversely the sparsity elsewhere.

In general, siphonophores occurred in 78% of the tows outside the lagoons and in 30% of those inside. This shows at once that the siphonophores were not evenly distributed throughout the water masses. An even stronger indication results from an examination of the distribution of *D. chamissonis* in Rongelap lagoon, where it was most abundant. Not only did it occur in only 53% of the tows, but in some of these catches it occurred in considerably greater numbers than in others. Obviously, then, this species tends to swarm. Such shoals (maximum of 29 to 32 eudoxids per cubic meter of water, Table IV) are not dense in comparison with the patches[14] of planktonic organisms frequently seen at the surface, but they are considerably denser than Stephensen's (1925) estimates for amphipods.

Systematic Considerations. Since so many of our specimens were

[12] Davis (1948), for example, reports 60,000,000 per liter in the Gulf of Mexico.

[13] Bigelow (1922; 1926: 205) reports upwards of 2.5 million large *Calanus finmarchicus* in what I judge to be a vertical meter net tow from 40–0 meters, which means perhaps upwards of 83 thousand per cubic meter of water.

[14] Recent work on the "scattering layer" (Hersey and Moore, 1948; Johnson, 1948) suggests a concentration of the larger zooplankton organisms (at depths of from 50 to 250 fms.) because of its diurnal vertical migration. This is similar to that observed in shallower areas by earlier workers (Russell, 1936; Clarke, 1934), although no indication is given of the numerical abundance of these organisms. However, the sort of patchiness referred to above has not been considered. Actually, a practical device (or devices) for sampling shoals of organisms of this sort from known levels or from a particular water mass has not yet been devised, but in time this should be possible, especially with the aid of the refined techniques used in delimiting water masses while working in the field (Ford, 1947).

small and not too well preserved, nothing can be added to what is already known, either morphologically or systematically, with the exception of three small (3–4 mm.) superior nectophores which apparently belong to a new species.

Galetta, Stechow 1921

Three rather poorly preserved superior nectophores, taken in separate tows near Rongerik and Bikini atolls, can be definitely referred to the genus Galetta, even in the absence of stems with permanently attached cormidia or of inferior nectophores with looped lateral canals. The nectophores are well rounded without any trace of ridges, the hydroecium is shallow and not clearly defined, and there are no basal teeth surrounding the opening of the nectosac. Commissural canals were not observed, but sufficient evidence has now accumulated to show that this is no longer a reliable character for distinguishing the superior nectophores in this genus from other calycophorids (Bigelow and Sears, 1937: 34, 36).

Galetta bigelowi n. sp.

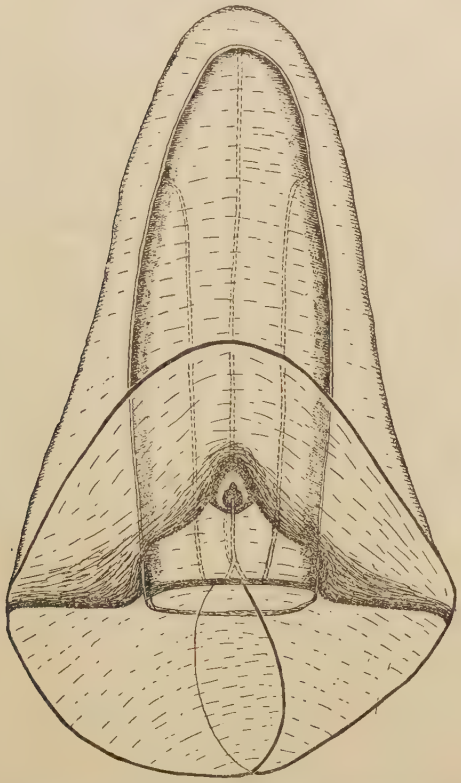
Figures 1 and 2

1 superior nectophore (type), CROSSROADS Plankton Station No. 270; 1 superior nectophore, CROSSROADS Plankton Station No. 300; 1 superior nectophore, CROSSROADS Plankton Station No. 408. (These specimens have been deposited in the U. S. National Museum.)

The three specimens listed above are so different in general appearance from all other members of the Galettinae that, despite poor preservation, it was at once apparent that they belonged to a rare or unknown species. To begin with, the general outline of the nectophore is definitely conical in dorsal and ventral views (Fig. 1) rather than tubular as in most species belonging to the genus. Viewed ventrally, the oblique ventral base, together with the two extraordinarily wide ventral lamellae (Fig. 1),[15] forms an almost complete circle, which, at least in much contracted preserved specimens, tends to surround the opening of the nectosac. Furthermore, in contrast to other species of Galetta, the oblique surface thus formed equals about one half the total height of the nectophore (including the lamellae). The lamellae, however, are not proportionately longer than in other members of the genus, although they are twice as wide. The hydroecium is a shallow indentation (Fig. 1). Just above it and projecting out into this depression is a minute somatocyst whose main axis in

[15] It is believed that an apparent variation in the size of the ventral lamellae of one specimen was due to distortion and shrinkage in preservation.

the crushed specimens at hand appears to be almost at right angles to the nectosac (Fig. 2). The shape of the somatocyst (Fig. 2) appears to be characteristic. The musculature of the nectosac resembles that seen in other members of the genus. There is no trace of the stem or other structures on any of the specimens.



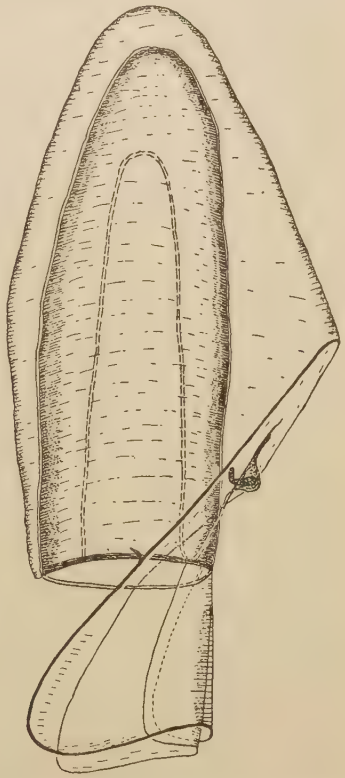


Figure 1. *Galetta bigelowi* n. sp. Ventral view of superior nectophore, somewhat restored, from the specimen taken in CROSSROADS Plankton Station No. 270.
Figure 2. *Galetta bigelowi* n. sp. Lateral view of superior nectophore, restored and somewhat diagrammatic, from the specimen taken in CROSSROADS Plankton Station No. 270.

The canal system in the genus Galetta appears to be extremely variable even among individuals of the same species. Although not definitely proven, it begins to look as if the younger individuals are apt to have canals of the *Diphyes* type which, as they grow older, develop the commissural canals usually considered as characteristic of the Galettinae (Browne, 1926: 68; Totton, 1932: 344; Bigelow

and Sears, 1937: 36). The three specimens at hand, all small, lack these. In addition, this species is unique in that the ventral canal splits into two short branches before entering the ring canal. At the point where the canal splits, the short pedicular canal enters from the stem and somatocyst. This appears to be fairly characteristic, if these three specimens can be taken as typical. Nevertheless, it should be borne in mind that there is considerable variability in *G. australis*, in this region. In the latter species, the lateral canals may enter the ring canal directly, they may enter the ring canal at the point of entrance of the ventral canal, or they may enter the ventral canal some distance above the ring canal (Bigelow and Sears, 1937: 36). The pedicular canal seems to have been overlooked in a number of instances, but re-examination of well preserved Albatross and Arcturus specimens of *G. australis* in the collection of the Museum of Comparative Zoology, together with drawings of *G. chuni* (Lens and Van Riemsdijk, 1908: pl. 9, fig. 78), of *Sulculeolaria quadridentata* (Bigelow, 1918: pl. 8, fig. 1), of *S. quadrivalvis* (Bigelow, 1931: figs. 195, 197), plus descriptions of the canal system (Browne, 1926), all seem to indicate that this canal enters the ring canal directly at the same point as the ventral canal or may enter the ventral canal just above the ring canal (Browne, 1926: 68). Whether a similar range of variation will be found in the present species, when more specimens are available, remains to be seen. Actually, in the three specimens in the CROSSROADS collection, none of which are very well preserved, the only variation seems to be in the relative height of the lateral canals. In one specimen they reach nearly to the apex, but in the other two they extend only about three quarters of the distance between the opening of the nectosac and the apex.

Two characteristics of the superior nectophores, i. e., the extraordinarily wide ventral lamellae and the peculiar shape of the somatocyst (Figs. 1 and 2), distinguish the present species from the other recognized members of the genus Galetta, namely *G. australis* Quoy and Gaimard (genotype), *G. chuni* Lens and Van Riemsdijk, and *G. meteori* Leloup.[16] Furthermore, I believe that the three specimens at hand cannot be referred to the questionable species, *G. turgida* Gegenbaur (1854), because they do not have the unique characters usually attributed to *turgida* (i. e., the single rounded ventral lamella and the absence of a somatocyst); in addition, they do not have the ridges on

[16] Totton (1932: 34) also lists *biloba* among the species of this genus, but Bigelow (1918: 419; 1931: 564) as well as Moser (1913, 1925) have relegated Sars species, *biloba*, to the synonymy of *G. australis* Quoy and Gaimard. Leloup's (1934) specimens of *meteori* were all so small that they may eventually prove to be the young of *australis* (Bigelow and Sears, 1937: 34).

the superior nectophores that he described. Therefore, they seem to belong to a new species, *Galetta bigelowi*, which is named for Professor Henry B. Bigelow in appreciation of the years I had the privilege to work with him.

For some time there has been considerable doubt as to whether Gegenbaur's (1854) *Diphyes turgida* could be definitely associated with any siphonophore found in recent years (Bigelow and Sears, 1937: 33), because his description of the anterior nectophore as having "eine dünne, abgerundete Lamella" (Gegenbaur, 1854: 443) distinguishes it from all other known siphonophores. Later, in the same paper, Gegenbaur (1854: 454) repeats his description of this character by saying "an der Mündung des vordern, so wie an jener des hintern Schwimmstücks eine vorstehende abgerundete Lamella." *D. turgida* was also described as lacking a somatocyst by both Gegenbaur (1854) and Sars (1859), although Chun (1885) figures one on a young superior nectophore, which lacks other distinguishing characters. In studying one of our specimens, the only one in which the overlapping ventral lamellae were undamaged, a first inspection revealed what appeared to be but a single undivided lamella. However, on closer examination two overlapping lamellae (Fig. 1) were actually found. Likewise, without using quite a high power of the microscope, the somatocyst would not have been obvious. Hence, both characters which make the species under consideration unique among siphonophores are such that they could have been overlooked easily. However, Gegenbaur's powers of observation and description have proven so accurate in most instances that it is hard to believe he erred on this occasion. Because his figure (1854: pl. 23, fig. 1) resembles, on a smaller scale, that of *G. australis* as drawn by Bigelow (1911: pl. 6, figs. 1, 3), it would seem that he probably had described damaged specimens of *G. australis* and that *G. turgida* should become a synonym of *G. australis*, as suggested tentatively by Bigelow (1911: 234, 238). This would appear reasonable, for *G. australis* is an extremely fragile species and is usually badly damaged in most plankton samples; in such cases the somatocyst is often destroyed completely (Bigelow and Sears, 1937: 36). Unfortunately, this solution does not seem possible in view of the fact that Gegenbaur (1854: 442) definitely states that the superior nectophore is "einem vierseitigen Körper, der nach vorn pyramidal sich zuspitzt."

The only recent author who figures a specimen believed to be *G. turgida* is Candeias (1929: 272–273, fig. 2). He suggests that his specimen is Gegenbaur's species owing to the very small somatocyst, but the figure otherwise resembles closely his drawing of *G. australis*. However, within the last few years, study of a considerable series has

shown that the somatocyst in *Galetta australis* (Bigelow and Sears, 1937: 36, fig. 26) may be quite variable in size (and may even be absent in preserved specimens). It now appears likely that Candeias' specimen actually may have been *G. australis* rather than *G. turgida*, as he suggested.

Totton (1932) reports *turgida* from the Great Barrier Reef, but without either figures or description. He also writes me that my description of the CROSSROADS specimens "sounds like a species with relatively large lamellae—identified tentatively with *Galetta turgida*" (Totton's letter dated 2 March 1949). This suggests that Totton's species may be the same as the one described above and here called *G. bigelowi*.

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NOTES ON DETERMINING THE DEPTHS OF SAMPLING IN SERIAL OCEANOGRAPHIC OBSERVATIONS

By

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ABSTRACT

In order to interpolate between thermometrically determined depths of sampling in serial oceanographic observations it has been customary to plot a curve of depth to wire length ratio against wire length. It is shown that a simpler and probably more accurate method consists of plotting wire length minus depth against wire length. In this method the surface wire angle is converted into a line of tangency to the curve which always terminates at the zero point of the graph. Furthermore, the limiting slope of this curve is more readily defined and utilized.

In oceanographic serial observations the determination of depth by means of an unprotected reversing thermometer is a completely standardized technique which requires no further elaboration. On the other hand, when only two or three unprotected thermometers are used on a deep cast, the interpolation for the depths of intervening Nansen bottle samples and temperatures presents a problem of somewhat greater complexity. This problem has become especially pertinent since the end of the war because of the limited supply of reliable unprotected reversing thermometers now available in this country. Closely related to it is the problem of extrapolation beyond the lowest thermometrically determined depth on exceptionally deep casts. The depth limit of an unprotected thermometer having a scale range of 60° C. and a pressure coefficient of 0.01° C. per meter is about 5,500 meters. Only an occasional thermometer has a pressure coefficient sufficiently small to permit the direct measurements of depths as great as 7,000 meters.

The procedure now generally used for calculating depths of sampling will be called the depth ratio method. This consists of plotting the ratio of thermometer depth to wire length (D/W) against wire length (W) and drawing a smooth curve through these points. The cosine of the surface wire angle is used as an additional point at the surface. Intermediate depths are obtained by multiplying the wire length by its corresponding ratio on the curve.[2]

[1] Contribution No. 488 from the Woods Hole Oceanographic Institution.

[2] Sverdrup, H. U., Determination of depths at which temperatures were measured and water samples collected, in, Scientific results of Cruise VII of the Carnegie during 1928–1929; Oceanography—1-A, Observations and results in physical oceanography. Publ. Carneg. Inst., No. 545: 15–18 (1944).

A different procedure, used by the writer in working up a number of Atlantis stations, involves less computation than the depth ratio method and is believed to be at least as accurate. Instead of the depth ratio (D/W), the depth difference ($W - D$) is plotted against wire length for the thermometrically determined points and a smooth curve is drawn through them. This curve must terminate at the zero point of the graph, thus, in effect, adding an inerrant point towards its construction. The surface wire angle is utilized by converting it to a line to which the curve becomes tangent at the surface. This is done in the following manner. Supposing the wire angle to have a cosine of 0.870, the line of surface tangency is drawn from the origin through a point with co-ordinates $W = 100$ and $W\text{-}D = 100 - 87 = 13$, or $W = 1000$ and $W\text{-}D = 1000 - 870 = 130$. Intermediate depths are found by interpolation along the curve and by the subtraction of the depth difference from the corresponding wire length.

A comparison of the two methods is best illustrated by the example shown in Fig. 1: the depth ratio and depth difference curves for a deep Atlantis station on which nine Nansen bottles were distributed between wire depths of 2,300 and 7,200 meters. Only two unprotected thermometers were available, each attached near its maximum depth. Since the wire angle is apt to be a crude measurement, the cosines and lines of surface tangency for angles 5° on either side of it were also plotted on the graphs.

These supplementary surface values bring out one of the major distinctions between the two systems. An error in the surface wire angle would radically change the depth ratio curve and would throw suspicion on the validity of the two thermometric points. On the other hand, even though the slope of the depth difference curve would be altered near the surface, the three points used for its construction would remain unchanged and only the accuracy of the wire angle would become open to question.

Another important difference between the two methods is found in the limiting slopes of the curves. The slope (λ) will be defined as equal to 0 when it is parallel to the vertical axis of the graph. For the depth ratio curve,

$$\lambda = \frac{d\left(\frac{D}{W}\right)}{dW} = \frac{W dD - D dW}{W^2 dW},$$

while for the depth difference curve,

$$\lambda = \frac{d\,(W\text{-}D)}{dW} = \frac{dW\text{-}dD}{dW}.$$

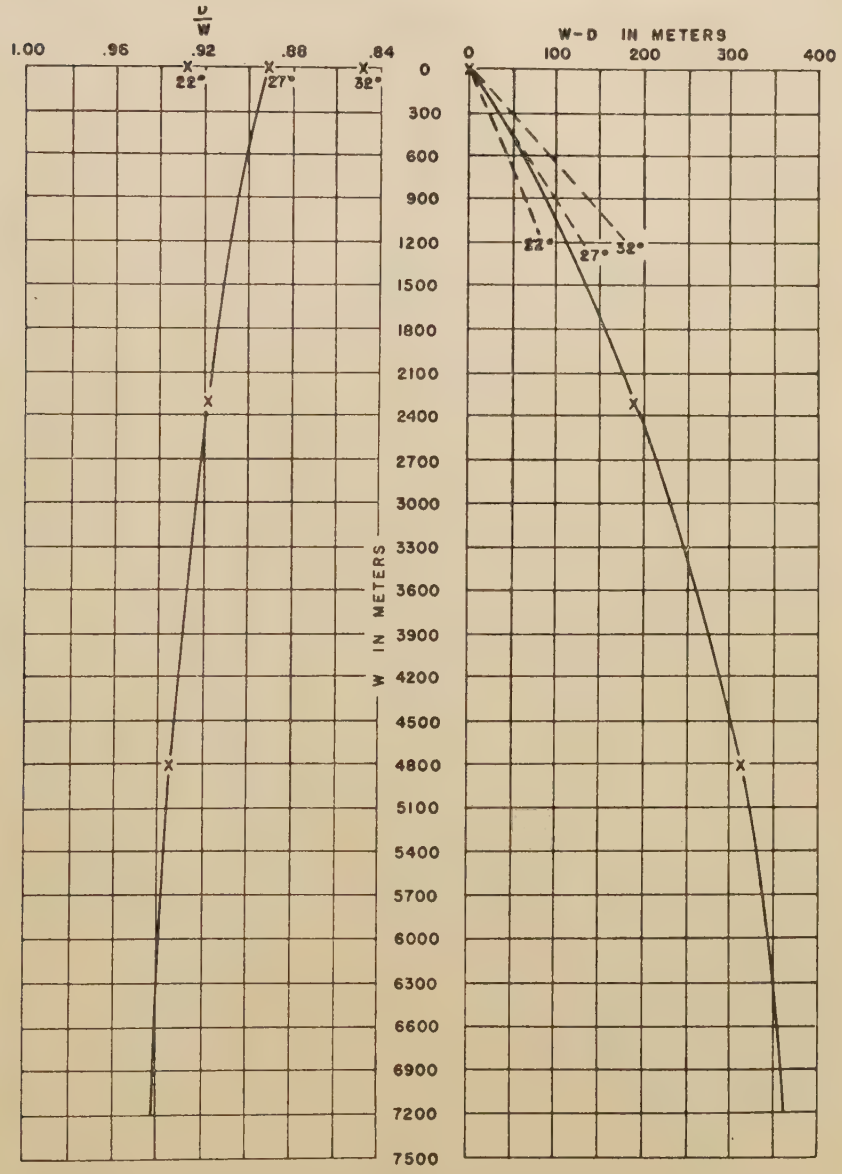

Figure 1. Depth ratio and depth difference curves for a deep Atlantis station.

The hydrographic wire reaches a limiting shape at any depth when it becomes vertical. This condition implies that $dD = dW$ at that point, resulting in slope values of $\lambda = \frac{W\text{-}D}{W^2}$ for the depth ratio curve and $\lambda = 0$ for the depth difference curve. It is evident that this curve characteristic cannot be utilized conveniently in the depth ratio method.

The question of curve slopes is closely related to the final step in the depth determination of serial observations. This is to ascertain whether the distances between sampling bottles are compatible with the wire distances between them. While in the depth ratio method these figures can be checked only after all depths have been computed, in the depth difference method the curve itself, when properly constructed, will eliminate the possibility of such discrepancies arising. In a correctly drawn curve the depth difference can never decrease with increasing wire length. This rule also provides a crude test for the accuracy of thermometrically determined depths in so far as it establishes a necessary but not sufficient condition for their relative horizontal co-ordinates.

Since the construction of any curve involves a considerable amount of personal judgement, errors in the interpolated values cannot be eliminated entirely. A comparison of the methods under discussion with respect to these errors should form an additional basis for assessing their relative merits. If the horizontal co-ordinates of the graphs are denoted by X, then for a given value of W, $D = WX$ by depth ratios and $D = W - X$ by depth differences. Thus, in the former method, an error in X will cause an error in depth which is directly proportional to the wire length, while in the latter method, an error in X will cause a depth error having the same magnitude at any wire length. Although on first analysis this points to a decided superiority on the part of the depth difference curve, an additional factor enters the picture.

A unit of X on the depth difference graph is generally several thousand times as great as on the depth ratio graph (2,500 to 1 in the example). This means that, for a similar displacement of the curves in units of X, the ratio curve will give a smaller depth error between 0 and 2,500 meters while the difference curve will give the smaller error beyond 2,500 meters. However, the greater reliability of the difference curve near the surface will compensate to some extent for its development of large errors in that range. Furthermore, the depth to which the ratio curve is superior will vary with the scale ratio of the two graphs and may be considerably less than in the example cited.

FOLLICULINIDS OF THE CHESAPEAKE AS NOMADS

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ABSTRACT

During experiments by the U. S. Fish and Wildlife Service and the Maryland Conservation Department on the fouling of oysters in Chesapeake Bay, shells exposed on the bottom were examined for folliculinids. Observations in the upper part of the Bay, at about 15 stations in 9 to 20 feet of water along some 40 miles from Choptank to Tochester from mid-May to mid-October, showed that settling began the last week of June, or occasionally mid-July, and continued until the last week of September; generally there was a decline in density during August and occasionally an increase in September with cooler water. Further down the Bay, shells were exposed off the mouth of the Patuxent River on "Parker Moore" bar in depths of 6 to 16 feet of water during 1944–1947; 1417 shells were examined, of which 243 bore folliculinids, with a much higher percentage of settling in deeper (26%) than in shallow water (6%). Exposures of shells on bottom were irregular, making comparisons of seasonal settling difficult, but settling did occur, though with considerable irregularity, during both winter and summer in each year. It is inferred that folliculinids are both sedentary and migratory at all times of year in the Chesapeake. Table I gives the data.

Folliculinids are the largest protozoans that make transparent tests, and in these they dwell and feed both by day and night upon suspended detritus, bacteria, minute plants and animals; other animals, in turn, feed upon folliculinids. Thus they too are a link in the complex food chain.

First seen in 1781 on the coast of Denmark, folliculinids were later found to be widely distributed all over the world. They are found mainly in the sea, though some are found in fresh water.

The older microscopists spoke of them as "bottle animalcules," since each was firmly anchored inside the bottom of the bottle-like test it had secreted, the test itself being firmly glued to dead or living objects. While the test serves as a protection, the mouth end of the folliculinid can be extended from the test for gathering food (Fig. 1). An adult within its test may revert to a simple larva-like form which divides into a posterior half that remains in the old test and an anterior half that swims forth to secrete a new test within which it develops into a new adult. Moreover, it was shown independently by Claparède and Lachman (1858), Wright (1858) and Andrews (1915) for marine forms, and by Penard (1919) for freshwater forms, that such animals may break loose as swimmers without dividing. Thus

folliculinids have two phases and are alternately sedentary and migratory.

The folliculinid literature indicates that they are known chiefly as sedentary organisms living in fixed dwellings. However, the extent to which they are permanent residents, or migrants, is evidenced only in the tributaries of Chesapeake Bay, where Andrews (1915, 1923) found that they were present in excessive abundance in the warm months on flowering plants in shallow water but that they all disappeared before the plants died down in autumn. This was the case from 1912–1949 inclusive.

For some years the Fish and Wildlife Service and the Maryland Conservation Department have carried on experiments to determine the periods of fouling by organisms such as barnacles, sponges, etc. Their approach to the problem was to put 25 to 50 clean oyster shell valves in a chicken wire bag with buoy attached, place it on the bottom for a week, and then lift it in order to examine the shells for attached organisms. Weather and other factors permitting, this procedure was followed week after week. In the Chesapeake, folliculinids fasten their tests mainly to oyster shells, which are the chief available objects on the bottom, so that sometimes the shells become covered with tests of several species. If these tests are sufficiently abundant they might interfere with the attachment of oyster spat, in which case they would be considered "fouling organisms" by the oyster biologists.

Regarding observations in the upper part of the Bay, we have the following information from Dr. P. A. Butler. Observations were made at about 15 stations in 9 to 20 feet of water along some 40 miles from Choptank to Tolchester from mid-May to mid-October. Here folliculinids settled on the shells of living oysters as well as on both surfaces of the empty shells. Settling did not begin until the last week of June, or occasionally mid-July, but it continued until the last week of September. Generally there was a marked decline in density during August, but occasionally there was a pronounced increase in density during September as the water cooled. Shells put down in October usually remained blank. In 1944 an exceptional absence of folliculinids occurred during the first three weeks of August at a station in Round Bay (Severn).

Further down the Bay, shells were examined by myself after they had been studied by oyster biologists at Solomons. These shells had been exposed on "Parker Moore," a large natural oyster bar off the mouth of the Patuxent whose position may be found in Grave (1912). The bar extends from near shore to the unusual depth of 46 feet, and hence the occurrence of folliculinids on this bar may be taken as indicative of what may occur on other bars which form a fringing reef

along the shores of the Bay and its branches. On "Parker Moore," shells were exposed near shore in six feet of water and also in a depth of 16 feet 500 feet further out. Records showed bottom temperatures from 9.2 to 26.6° C. and salinities from 9.3 to 19 parts per mille.

Ten shells from each wire bag were studied under the binocular. The colored tests stood out against the white inner face of the shells so that the prevailing species were recognizable; even the early settling stages showed as blue smears where the swimmers spread out before making tests. However, there is a distinct disadvantage in the use of dry shells due to occasional curling or peeling off of smears or completed tests.

Contrary to expectations, few shells showed folliculinids: only 243 (17%) out of a total of 1,417 shells bore these organisms. However, in deeper water the percentage was greater than that in shallow water: 202 out of 760 (26%) as compared with 41 out of 657 (6%). Shells were examined from the last two months of 1944, from ten months of 1945, twelve of 1946, and eight of 1947. The percentages per year for 1945, 1946 and 1947 were 21, 30 and 35 respectively for deeper water, 21, 3 and 7 respectively for shallow water. In deeper water the shells were exposed for 15, 23 and 11 weeks in these same three years (a total of 49 weeks) with folliculinids found in 9, 14 and 6 weeks respectively (a total of 29 weeks). In shallow water the shells were exposed 13, 22 and 11 weeks (total 46 weeks), with folliculinids found in 6, 4 and 1 weeks, or a total of only 11 weeks out of the entire 46. Thus it is apparent that there was a greater paucity of settling in the shallow water.

A comparison of the settling in winter with that in summer is complicated by the fact that duplicate bags were put out in the summer and were recovered fairly regularly, while in winter there was often a failure to recover the bags because of weather conditions and other factors. Consequently, the summer yielded many shells that had been down for only a week or so, while the winter yielded fewer shells, some of which had been exposed for much more than a week. Seldom were all ten shells set with folliculinids; some showed none, others few, and still others many, which we have indicated generally by the letters *A* to *D* in Table I.

There was no correlation for the settling of folliculinids with that of other organisms. While most shells showed some barnacles and bryozoa, and some bore oyster spat, algae, hydroids and egg capsules of gastropods, folliculinids did and did not occur with them.

The data are summarized in the accompanying table. The arabic numerals show the number of days the shells were exposed, and the letters *A*, *B*, *C*, and *D* are used to indicate when folliculinids were

TABLE I. Tabulation of Results from an Examination of Ten Oyster Shells Taken at Random from Bags of 20 to 50 That Had Been Exposed the Number of Days Represented by Arabic Numerals. The Presence of Folliculinids Is Indicated as Follows: *A*. Mere Trace on One or More Shells; May Be Just One or More Smears as Evidence That Settling Has Begun. *B*. Few on a Few Shells. *C*. Hundred or So on One or More Shells. *D*. Several Hundred on Many Shells.

Shallow Water

Months/Years	*1944*	*1945*	*1946*	*1947*
I.	—	—	—	30.19.
II.	—	—	—	14.20,*A*.
III.	—	158,*C*.117,*C*.7.13.	29,*D*.	16.
IV.	—	9.10.10.	12,*A*.15,*B*.12.	16.
V.	—	58,*B*.9.	9.17.	27.
VI.	—	—	17.7.6.6.	34.12.
VII.	—	—	7.16.6.6.15.39.8.26.26.	7.7.6.
VIII.	—	—	9.9.9.9.8.10.10,*A*.10,*A*.	7.
IX.	—	—	103,*D*.6.6.5.5.11.15.	—
X.	—	—	8.	—
XI.	11.	—	34.7.6.18.	—
XII.	42,*B*.	—	6.7.	—

Deeper Water

	1944	*1945*	*1946*	*1947*
I.	—	—	26,*B*.26,*B*.	30,*B*.18,*C*.
II.	—	—	15,*B*.	12.20,*A*.
III.	—	—	—	22,*A*.
IV.	—	—	12,*B*.12.	16.14.
V.	—	8.8.8.	10.11.6,*A*.	—
VI.	—	14.11.10.	25.7,*A*.	12.11.
VII.	—	9.6.7,*A*.	15.15.8.8.8,*A*.8,*A*.	13.7.
VIII.	—	12,*B*.6,*A*.8,*A*.7,*A*.	4,*A*.4,*A*.8,*B*.8,*B*.9,*D*.9,*C*.	7,*B*.
IX.	—	7,*B*.	7,*C*.7,*B*.5,*B*.5,*C*.6,*D*.	—
X.	—	7,*A*.14,*A*.15,*A*.	16,*D*.	—
XI.	—	14,*A*.	3,*A*.7.7,*B*.	—
XII.	—	18.	7.7.7.	—

found to be fastened to the shells and to indicate the relative abundance, *D* being the maximum.

Obviously folliculinids settled on the shells both in winter and in summer, but during cold weather the records were sparse, so that evidence of attachment of folliculinids to shells that had been exposed for only a few days, as was sometimes the case in warmer months, is lacking.

If reference is made to Table I, particularly to the data for August 1946 for both shallow and deeper water, it will be seen that many exposures were examined and that there are indications of settling only late in the month in shallow water but all through the month in deeper water. Hence, since there is a diverse amount of settling in months as well as years, we may infer that folliculinids in the Chesapeake occur at all times of the year in both the attached and drifting phases; however, as a population, the folliculinids are essentially nomads visiting shore regions in great swarms during the warmer months.

DISCUSSION

Folliculinids in the Chesapeake have a wide distribution, and it is inferred that the individuals frequently change their locations, since transformation and migration are fundamental features of the life cycle of all folliculinids. Throughout the Chesapeake the density of occurrence varies greatly, not only from place to place but in each place from time to time. Thus in late summer there is a maximum display in shallow water, while during the rest of the year there is evidence of intermittent occurrence in variable abundance which differs from year to year.

In the laboratory it was seen that swimmers advanced so slowly that they would progress scarcely 50 feet under their own power before settling down, yet tide and current may carry them far. In the experiments on "Parker Moore," settling on one part of the reef was not always coincident with settling in another part, and hence there appears to be no vast migration. As further evidence of this we might point to the often observed fact that masses of folliculinid tests are found along shore on only certain sections of an area of vegetation, the intermediate areas being quite free of any. However, absence of tests need not mean that no swimmers were in that region, for certain solids, such as shells and leaves covered with slime and detritus, are not suitable for attachment. For example, *Metafolliculina andrewsi* Hadzi rejected certain substances (Andrews, 1915). Furthermore, although clean plants destitute of tests may seem the same as those that are crowded, such things as local temperatures or chemical factors associated with springs or type of bottom may make such plants inimical to settling. Almost invariably some tests were found on shells that had been exposed for some weeks, while in periods of greatest abundance it was sufficient for them to be down but a week, or even three days, to accumulate tests; however, in shallow water there were records of no settling in 34 and 39 days.

The maximum swarming of swimmers occurs in late summer at high temperatures when other shallow water marine forms invade brackish

waters and commingle with fresh water forms. In this temporary exuberance of life, folliculinids crowd along the shore and present certain aggregations that may be of significance.

As seen in Fig. 2, *Metafolliculina andrewsi* Hadži sometimes fixes its tests over the uniform surface of an oyster shell in irregular fashion, scattered individuals living near together or far apart, with no orientation or evident connection with one another. But in the maximum period, shells and plants near shore show the tests aggregated into conspicuous clumps, as on the leaf of potamogeton shown in Fig. 3. Often such clumps are placed with reference to some part of the leaf. These groupings are made over and over again on plants as well as in the laboratory; as seen in Fig. 4, they have settled on a glass slide in an aquarium after swimmers had escaped from tests established on the leaves. In these groups the individuals stand side by side or in radiating fashion close together; though they may cluster in numbers as high as 200, the number per group is limited, with the complex often being much smaller. While some observers thought that such accumulations were due to an increase of one pioneer individual, we found, in the laboratory, that all members of the group are of about the same age and that they settled down at about the same period; presumably the ones that settled first attracted others until many were parked together, thus leaving few unoccupied spaces midst the whole.

The possible import of this aggregation may be that it favors conjugation, which has not been observed in folliculinids though seen in their close relatives, the stentors, where two adults coalesce in the peristomial region and exchange nuclear materials before separating. Obviously such clumping would increase the chances of two joining, and we suggest, therefore, that this clumping is comparable to the "agglutination" in paramecia, where many adhere for a time and ultimately join in pairs. In both folliculinids and paramecia there are secretions involved in aggregation.

That conjugation has not been detected in folliculinids may be due to its occurrence only at certain hours of the day or night as in some paramecia. But failure to detect conjugation may be due especially to its probable rarity, since we expect conjugation to take place between mating types only. Despite the crowding in clumps, it may take many successive groupings to finally bring the right mating types into juxtaposition, especially if there be several mating types.

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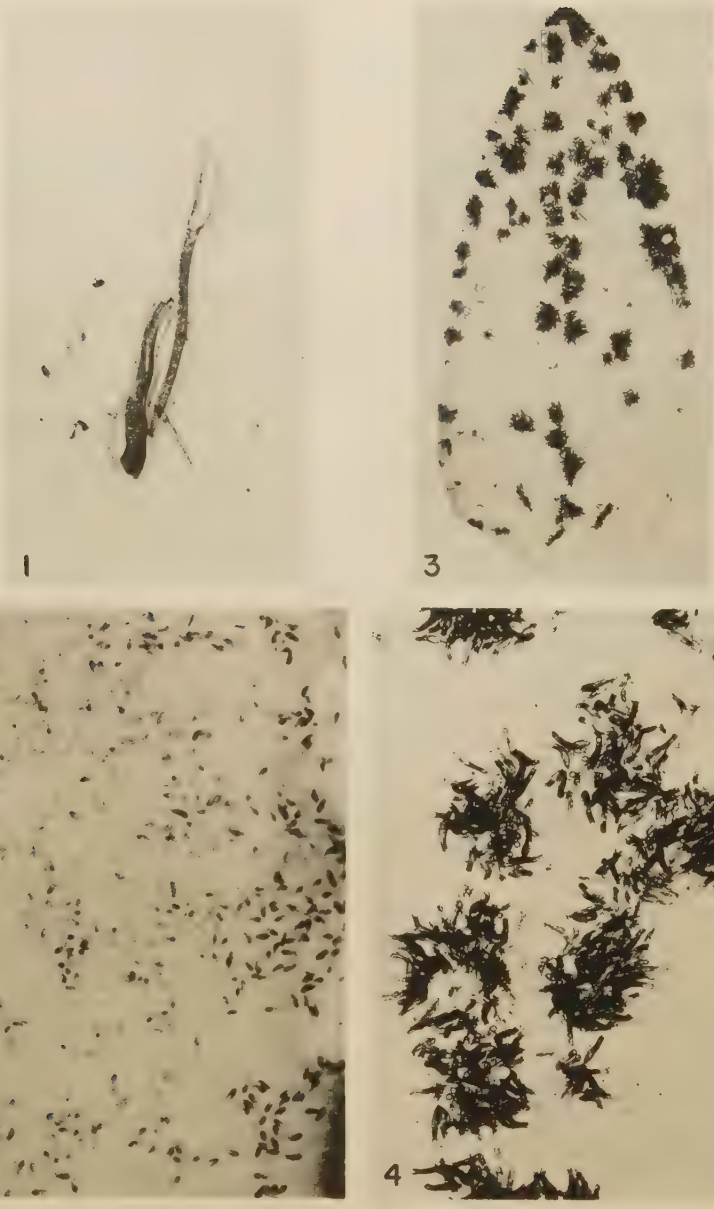

Metafolliculina andrewsi Hadzi, photographs by John S. Spurbeck. Figure 1. Two individuals enlarged, one contracted in its test but about to protrude, the other extended, with its long feeding lobes outside the test; on leaf of Elodea from north of Baltimore. Figure 2. A small variety scattered thickly over part of an oyster shell taken VI/19/42 by Gorden Gunter in upper part of Oransas Bay, Texas; salinity 20.02 parts per mille. Figure 3. Preserved leaf of potamogeton, from Severn River, with clusters of individuals near edges and midrib. Figure 4. Clumps formed on slide in aquarium by the settling of swimmers from leaves; enlarged from preserved specimen.

EXPERIMENTAL STUDY OF THE PHOSPHORUS CYCLE IN FERTILIZED SALT WATER[1]

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ABSTRACT

The rates at which phosphorus is (1) assimilated by phytoplankton, (2) released into solution from dead cells, and (3) regenerated to inorganic state, were measured in outdoor concrete tanks containing sea water fertilized with inorganic phosphate and nitrate. Bottles wrapped in black cloth and bottles exposed to the light were filled with the tank water and suspended in the tanks; the three rates in the P cycle were calculated from the observed changes in the concentrations of inorganic and particulate P in the bottles. The maximum recorded rates were: assimilation = 0.36 μg-at. P/L of sea water in the tanks/day; solution = 0.38 μg-at./L/day; regeneration = 0.13 μg-at./L/day. In 18 series of measurements, during which phytoplankton increases predominated over decreases, the following relations were observed between the rates of phosphorus transformations and the size and absolute change of size of the phytoplankton populations: (1) The rate of phosphorus assimilation was significantly correlated with the size of the phytoplankton standing crop and showed an even stronger dependence upon the increment of growth. (2) The rate at which particulate organic phosphorus was released into solution was intimately related to the size of the standing crop and was independent of the change in population size (which in most cases was an increase). (3) The regeneration of dissolved inorganic phosphate from dissolved organic phosphorus depended upon the phytoplankton standing crop and showed no relation to the change in population size. If attached algae were allowed to grow on the sides and bottom of the tanks, in less than one month they removed three-fourths of the added phosphate from the water-phytoplankton system. Where attached algae were largely prevented from growing, four-fifths of the phosphorus originally present was detected in the water at the end of four weeks.

Our understanding of the dynamics of biological productivity is measured by our knowledge of certain rates of transfer of matter and energy in the environment (Clarke, 1946). The productivity of most aquatic environments depends heavily upon the growth and maintenance of the phytoplankton, and this in turn is frequently limited to the rates at which phosphorus is regenerated and assimilated (cf. Ketchum, 1947). The rates of these processes in the cycle of phosphorus thus assume the greatest theoretical interest. Furthermore, a knowledge of the rates of assimilation and regeneration of plant

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nutrients such as phosphorus is essential for the most intelligent direction of a program of fertilizing natural waters, salt or fresh. In spite of their cardinal importance from the practical as well as academic standpoint, the magnitude of such rates remains almost completely unknown. Our ignorance of these matters can probably be attributed largely to the difficulties of measurement.

Redfield, Smith and Ketchum (1937) have calculated the net or minimal rates of the phosphorus metabolism in a column of water in the Gulf of Maine on the basis of measurements made at three-month intervals throughout the year. Hutchinson (1941) has estimated the average minimal rates of regeneration and sedimentation of phosphorus in Linsley Pond over a period of several weeks in the summer. The rates arrived at in both of these researches are averages for relatively long periods of time and are minimal only.

The purpose of the present investigation was to make approximately accurate measurements of the absolute rates at which phosphorus passes through its cycle of assimilation, solution and regeneration, and to relate these rates to the standing crop and growth rate of the phytoplankton population. The studies were conducted in fertilized sea water in outdoor concrete tanks at the Woods Hole Oceanographic Institution. These experiments form part of a study of productivity in salt waters, initiated and guided by George L. Clarke. Some results of this project have been discussed by Edmondson and Edmondson (1947) and by Pratt (1949), while others are in preparation.

METHODS

Inorganic phosphate concentration, determined by the modified Deniges-Atkins method (Wattenberg, 1937), was measured in a Klett-Summerson photoelectric colorimeter. All determinations were made exactly five minutes after addition of the reagents, and correction for salt error was applied. Concentrations are expressed as microgram-atoms of phosphate phosphorus per liter (μg-at. PO_4P/L).

Particulate Organic Phosphorus. The method employed is that of Redfield, Smith and Ketchum (1937), except that the intensity of the blue color was measured in a Klett-Summerson photoelectric colorimeter exactly five minutes after addition of the molybdate and stannous chloride reagents. Concentrations are expressed as μg-at. PO_4P/L.

Total Phosphorus. In the hope of following changes in the concentration of the dissolved organic phosphorus fraction and of keeping a balance sheet of all phosphorus in the system, Harvey's (1948) procedure for estimating total phosphorus was tried. However, this method frequently gave readings of "total" phosphorus which were

less than the sum of the inorganic and particulate fractions. Moreover, in various preliminary tests Harvey's method did not yield altogether satisfactory results. Therefore, until the method's effectiveness in detecting all the organic phosphorus has been fully demonstrated, it seems wise not to place too much reliance in the absolute values of the measurements, although the close agreement between readings of identical samples warrants considerable confidence in the relative values obtained. Concentrations were determined in a Klett-Summerson photoelectric colorimeter and are expressed as μg-at. PO_4 P/L.

Phytoplankton. The standing crop of phytoplankton was measured by the concentration of chlorophyll. I am indebted to W. T. Edmondson for the chlorophyll measurements, which he made in connection with experiments being conducted simultaneously with those reported here. The method is that described by Edmondson and Edmondson (1947), with the exception that the Klett filter No. 66 was replaced by a Farrand filter of narrow transmission range centered on the peak of absorption for chlorophyll *a*. The approximate calibration factor is one unit on the Klett scale = 0.26 mg. chlorophyll *a*/m^3, but since this may be slightly revised upon recalibration of the photocolorimeter, the chlorophyll concentrations are given in terms of Klett units.

In this investigation the importance of the phytoplankton standing crop and growth rate lies in the relations of these variables to the phosphorus cycle. The absorption of phosphate by the phytoplankton is a process intimately connected with photosynthesis. For this reason and because of the role of chlorophyll in photosynthesis, the use of chlorophyll concentration as an index of the phytoplankton population is particularly appropriate for our purpose.

THE MEASUREMENT OF RATES IN THE PHOSPHORUS CYCLE

Procedure. The concrete tanks, described by Edmondson and Edmondson (1947), had been filled with sea water for two summers previous to the present studies. Thus it seems likely that at least the principal exchanges of substances between water and concrete had already occurred before these investigations were begun. By the use of wooden partitions, the tanks were divided into four compartments, each being 2.74 meters long x 1.42 meters wide. On August 3, 1948, each of the four tanks was filled to a volume of 4.5 m^3 with sea water ($S°/_{oo}$ 32.42) pumped from the harbor and passed through a No. 10 bolting silk net (mesh aperture diameter = 134 μ) to remove everything larger than small zooplankters. On the morning of August 6, Tanks 1 and 2 were fertilized with Reagent $Na_2HPO_4 . 12H_2O$ in an

amount calculated to raise the inorganic phosphate phosphorus concentration by 5 μg-at./L; Tanks 3 and 4 received the same amount of phosphate plus Reagent $NaNO_3$ calculated to increase the nitrate nitrogen concentration by 80 μg-at./L. The ratio of added nitrogen to phosphorus was thus the average ratio in which they occur in marine plankton (Sverdrup, Johnson and Fleming, 1942). The observed increases in inorganic phosphate concentration resulting from the fertilization were, in Tanks 1–4 respectively, 4.87, 4.99, 4.61 and 5.11 μg-at./L. Nitrate concentration was not measured. On August 23 Tanks 1 and 2 were fertilized with Reagent $NaNO_3$ in an amount calculated to raise the nitrate nitrogen concentration by 80 μg-at./L.

Throughout the period in which experiments were conducted (August 6–September 1), the sides and bottom of Tank 4 were scraped with a stiff bristle brush every morning immediately after collecting the water samples. The other tanks were not thus treated, so that a thin mat of attached algae developed on their walls.

In the photosynthetic plankton,[2] the most abundant forms were *Prymnesium* sp. (Chrysophyceae), *Thalassiosira nana* (Diatomaceae), and *Nannochloris coccoides* (Chlorophyceae). Also frequently observed were *Gymnodinium punctatum*, *Glenodinium* sp. (Dinophyceae), *Platymonas* sp. (Chlorophyceae) and *Olisthodiscus luteus* (Xanthophyceae). The flora of Tanks 1 and 2 were quite similar, with *Prymnesium* usually the dominant form. In Tanks 3 and 4, *Nannochloris* became the most abundant form during the latter half of August, and throughout the last week it constituted more than 90% of these populations. During the first two weeks, cell counts in Tanks 1 and 2 rarely exceeded 2 million cells/L, and in Tanks 3 and 4 they were generally less than 5 million cells/L. The densest populations occurred at the end of August, with the following approximate maxima: Tank 1, 7 million; Tank 2, 5 million; Tank 3, 250 million; and Tank 4, 400 million cells/L.

This study is concerned with the rates of the following three processes in the phosphorus cycle: step 1, assimilation—the rate at which dissolved inorganic phosphate is taken up by the phytoplankton; step 2, solution—the rate at which the particulate phosphorus of dead cells is released as dissolved organic phosphorus; and step 3, regeneration—the rate at which the dissolved organic fraction returns to the inorganic phase. The term regeneration is thus used in a somewhat restricted sense. It applies only to the conversion, *in situ*, of organic compounds in solution to inorganic state. It does not refer here to

[2] Daily plankton identifications and counts, following centrifugation of fresh samples, were carried out by E. M. Hulburt and Albert Rosenberg.

the process of "solution" (step 2) nor to the influx of new supplies of phosphate through water movements.

The difficulty in measuring these three rates is that at least two of the processes occur simultaneously; the problem is to stop the cycle at one point so as to allow a measurable accumulation in one of the phosphorus fractions. Ketchum's (1939a) discovery that *Nitzschia* cultures would not assimilate phosphate in the dark (unless they were phosphorus deficient) apparently provides a means of arresting the cycle, with the accumulation of phosphorus in the dissolved inorganic fraction.

Under certain conditions this cessation of phosphate assimilation in the dark can be detected in natural populations that are adequately supplied with phosphorus. An earlier paper (Pratt, 1949) describes a marked diurnal fluctuation in inorganic phosphate values (high in the morning, low in the afternoon) observed in a salt pond after fertilization with superphosphate. This phosphate pulse is ascribed to a continuous (day and night) supply of phosphate from the fertilizer on the mud bottom, coupled with its discontinuous consumption by the phytoplankton during the hours of daylight only. These observations suggested the possibility of determining the regeneration rate by noting the increase in inorganic phosphate during the night in the open water of the tanks. Any detectable increase in the particulate fraction during the day would then represent the excess of assimilation over the solution of phosphorus from dead cells.

Accordingly, early morning and evening measurements were made of the dissolved inorganic and the particulate organic concentrations in the fertilized water of the tanks. In general, the inorganic fraction decreased by day, was restored by night, and these changes were mirrored in the concentrations of particulate phosphorus. The diurnal fluctuations were so slight, however, that their use for the reliable estimation of rates does not seem possible.

Under the conditions in the tanks it was necessary, therefore, to prolong the period of darkness artificially in order to permit a more accurately measurable accumulation of inorganic phosphate. This was done by the "dark and light bottle" technique widely used in the measurement of photosynthesis.

After thorough stirring of the tanks with an oar, clear glass-stoppered bottles of about 200 ml. capacity were filled by siphoning from a gallon sample collected approximately six inches below the surface. In siphoning, the water was passed through netting of such a mesh as to exclude any large clumps of detritus. Half of the bottles were then wrapped in several thicknesses of black cloth and, together with those exposed to the light, were suspended in the middle of the tank at

mid-depth. The concentrations of inorganic phosphate, particulate phosphorus and chlorophyll in the open water were determined immediately, using the remainder of the gallon sample. This sampling was always done between 9 and 9:30 A. M., with one exception (at 10:15). Forty-eight or 72 hours later the dark and light bottles were pulled up and their contents analyzed for dissolved inorganic and particulate organic phosphorus. At the same time the concentrations of these two phosphorus fractions and that of chlorophyll in the open water of the tanks were determined.

The rate of regeneration is measured by the increase in inorganic phosphate in the dark bottle during the two- or three-day period. The decrease of particulate organic phosphorus in the dark provides a measure of solution (step 2 in the cycle). The rate of assimilation can be measured in either of two ways. (1) It can be measured by changes in the particulate fraction. Since an increase in particulate phosphorus in the light bottle represents the assimilation of phosphate by the plankton in excess of solution, to that increase must be added the amount of solution, as measured in the dark bottle. (2) Similarly, the assimilation rate can be obtained from the decrease in inorganic phosphate in the light bottle, plus the amount of regeneration as observed in the dark bottle. This second method has been employed by Edmondson and Edmondson (1947).

If we introduce Δp for the change per day in the concentration of particulate organic phosphorus, and Δi for the change per day in the concentration of dissolved inorganic phosphorus, the scheme for measuring the rates can be expressed concisely as follows:

assimilation rate (step 1) = Δp in light bottle $-$ Δp in dark bottle, or
Δi in dark bottle $-$ Δi in light bottle
solution rate (step 2) = $-$ Δp in dark bottle
regeneration rate (step 3) = Δi in dark bottle

In the equations given for assimilation rate, Δp in the dark bottle and Δi in the light bottle must be preceded by minus signs because their values are ordinarily negative. The summation of terms in each of these equations thus gives the total rate.

Twenty-two series of measurements following this plan were conducted, according to the following schedule: Experiments in all four tanks August 6–9, 11–13, 20–23 and August 30–September 1; experiments in Tanks 1 and 2 alone during August 23–25, 25–27 and 27–30.

The described method for measuring rates in the phosphorus cycle involves three assumptions.

1. *There is no loss of phosphorus to the walls of the bottles.* Apparently this assumption did not hold perfectly. Judging from

measurements made with Harvey's method, there was usually a slight decrease in total phosphorus in the bottles during the experiments, amounting to .05 μg-at./L. per day. The loss of inorganic phosphate from sea water stored in bottles is a familiar occurrence and probably can be attributed to a film of bacteria firmly attached to the walls of the vessel. Harvey (1948) has discussed this phenomenon and has given evidence suggesting that dissolved organic phosphorus may be adsorbed on a clean glass surface. It is not known what phosphorus fraction or fractions suffered the apparent losses in the present study. However, in 11 of the 22 experiments, the amount of detectable inorganic phosphate decreased in the dark bottle, which suggests that at least a part of the total phosphorus lost was inorganic. This is perhaps a serious defect in the bottle method, but it appears to be unavoidable. The result is that regeneration rates estimated from the change in inorganic phosphate in the dark bottle are minimal.

2. *The phytoplankton does not assimilate phosphate in the dark.* The basis for this assumption is the work of Ketchum (1939a) with laboratory cultures of *Nitzschia closterium.* Whether the populations of the tank water did or did not assimilate phosphorus in the dark cannot be stated with certainty. The loss of inorganic phosphate in dark bottles discussed above might be interpreted as evidence of phosphorus assimilation by the phytoplankton, but it seems likely that at least a considerable part of this loss can be ascribed to the bacterial film. The only unequivocal indication of phosphorus uptake in the absence of light that can be deduced from the existing data is an increase in particulate organic phosphorus in the dark bottle. In the course of 22 experiments this occurred only five times: During the first series of experiments (August 6–9) immediately after fertilizing, particulate phosphorus in the dark bottle increased in three of the tanks; in the second series (August 11–13) such an increase was again noted in one of the tanks; and immediately following the addition of nitrate to Tanks 1 and 2 on August 23, a similar increase was observed in Tank 1. The first four instances of phosphate assimilation in the dark occurred in populations which presumably had not yet restored an initial phosphorus deficiency (cf. Ketchum 1939a). The fifth case illustrates another phenomenon described by Ketchum (1939b). Within certain limits the rate of phosphorus uptake by Ketchum's *Nitzschia* cultures depended upon the concentration of nitrate. Apparently the nitrate fertilization of August 23 so accelerated the rate of phosphorus assimilation temporarily that in Tank 1 this process was allowed to go forward even in the dark.

That the phytoplankton did not usually assimilate phosphate in the dark cannot be proven, but every instance in which the assumption

demonstrably did not hold can be explained on the basis of the temporary effects of phosphorus deficiency or increased nitrate concentration.

3. *The rates of solution and regeneration in the light bottle are the same as those in the dark bottle.* In the absence of any evidence bearing on this assumption, its validity can be judged on theoretical grounds only. Quite possibly light affects phytoplankton and bacterial populations in various ways which influence phosphorus solution and regeneration. For example, Newcombe (1940) suggests that living phytoplankton cells release inorganic phosphate into solution by night, but this hypothesis lacks support from experimental evidence. The animal population may be important also in this connection. Under natural conditions in the sea, light intensity may influence the rate of feeding by the zooplankton and presumably the rate of excretion of phosphate. It is a significant fact, therefore, that the number of macroscopic animals in the tanks was negligible; indeed, no zooplankters visible to the unaided eye were observed during the period of study. Unidentified species of rotifers and nematodes occasionally appeared in small numbers. Aside from these, the plankton fauna consisted of flagellate and amoeboid protozoa which rarely attained numerical importance. The effects of the light-influenced activities of this animal population on the phosphorus cycle cannot be assessed, but probably they were never significant. At least we can conclude that such effects resulting from the activities of macrozooplankton were absent in the tanks.

Degree of Agreement Between Independent Measures of Assimilation. It will be recalled that the changes in dissolved inorganic and particulate organic phosphorus in dark and light bottles yield two more or less independent measures of the rate of assimilation, *viz.* Δp in light $-$ Δp in dark, and Δi in dark $-$ Δi in light. Since one of these methods depends in part upon the solution rate ($-$ Δp in dark) while the other involves the regeneration rate (Δi in dark), a comparison of the assimilation rates as measured by the two methods furnishes a critical test of the consistency of the dark and light bottle method. The relationship between the two measures is shown in Fig. 1, in which the least squares line has been fitted to the data from the 22 experiments. The correlation coefficient is .735, which is well above the 1% level of significance. In other words, in only one case in one hundred would 22 sets of data yield a correlation coefficient as high as .735, by chance alone. Of the two measures of assimilation rate, that derived from changes in the particulate fraction is regarded as the more trustworthy, since a decrease in inorganic phosphate is at best an indirect measure

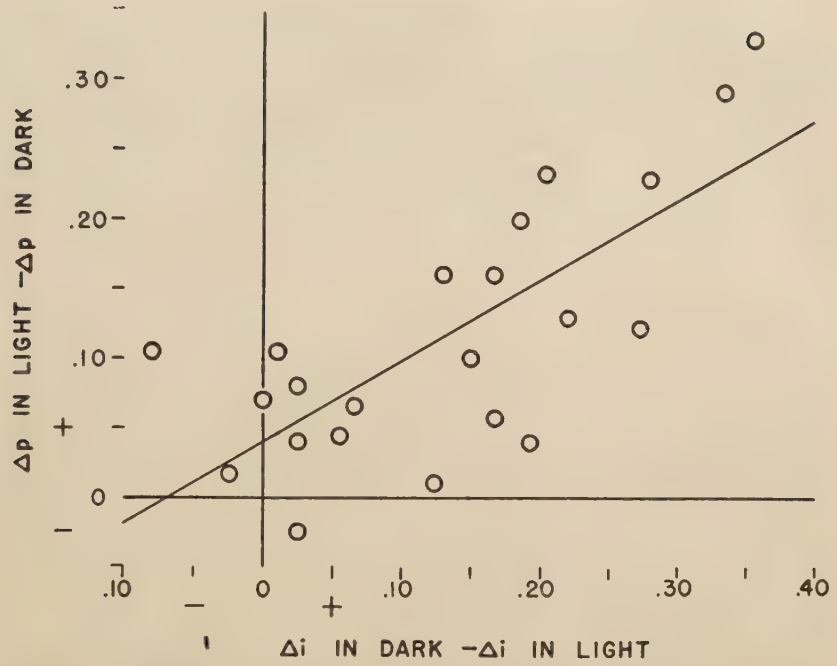

Figure 1. Correlation between two independent measures of phosphorus assimilation rate, in μg-at./L/day.

of assimilation, and there is reason to believe that some inorganic phosphate is lost to bacteria on the walls of the bottles.

Comparison of Phosphorus Changes in the Light Bottle with Those in the Open Water. By the dark and light bottle method one can measure directly the rates of phosphorus conversions only as they occur within the experimental bottles. One must then meet the objection that, for marine phytoplankton, the interior of a small, tightly-stoppered bottle is a habitat somewhat less than likely. Rates of phosphorus transformations within the bottles are of little interest except in so far as they represent conditions in the larger environment—the open water of the tanks, in the present study. Ideally, the interrelations of phytoplankton and water in the light bottle should be identical to those in the open water. For example, the changes in concentrations of inorganic phosphate and of particulate organic phosphorus in the light bottle should be the same as those in the open water. A moment's thought will show that the following relationship is also to be expected. Since an observed decrease in inorganic phosphate in the

open water represents the excess of assimilation over regeneration, the rate of that observed decrease should equal the rate of phosphorus assimilation in the light bottle *less* the regeneration rate. Thus we have the bases for three comparisons between the light bottle and the open water, and each of these provides a measure of the usefulness of the dark and light bottle method for estimating the rates of phosphorus transformations in the larger environment.

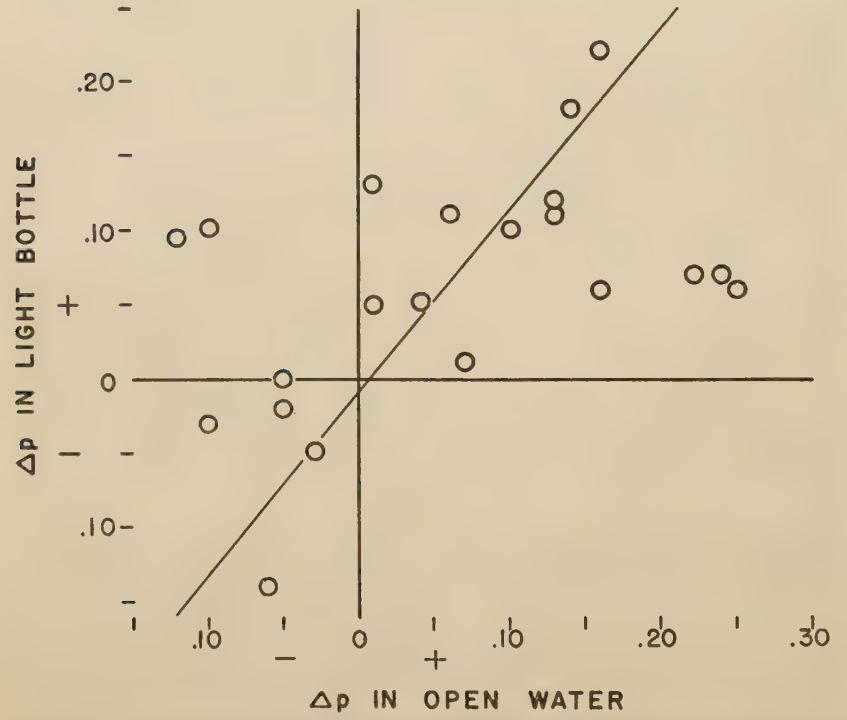

Figure 2. Correlation between rate of change of particulate phosphorus concentration in light bottles and that rate in the open water, in μg-at./L/day.

The correlation coefficients for these relationships are as follows: (1) for Δp in open water *vs.* Δp in light bottle, $r = .566$, which is significant to the 1% level of probability; (2) for Δi in open water *vs.* Δi in light bottle, $r = .596$, significant to the 1% level; (3) for Δi in open water *vs.* Δp in light bottle $-$ Δp in dark bottle $-$ Δi in dark bottle, $r = .461$, significant to the 5% level. The less satisfactory agreement in the third correlation as compared to the first two can probably be laid to inaccuracies in the measurement of regeneration,

for, as we have seen above, there is reason to believe that changes in inorganic phosphate in the dark bottle give erroneously low values for the regeneration rate. The plots of these three correlations, with the least squares line fitted to each, are given in Figs. 2, 3 and 4.

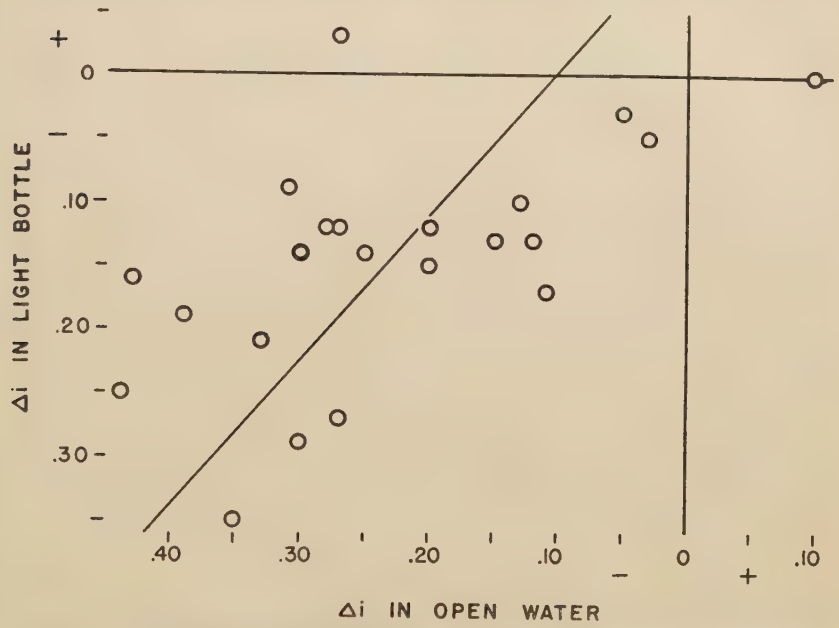

Figure 3. Correlation between rate of change of inorganic phosphate concentration in light bottles and that rate in the open water, in μg-at./L/day.

The line of regression for phosphorus uptake as measured by changes in the particulate fraction (Fig. 2) shows nearly a 1 : 1 ratio between open water and light bottle, and it almost passes through the origin. This indicates that in so far as phosphorus assimilation is concerned, environmental conditions in the light bottle were statistically the same as the average of conditions throughout the tank.

A different sort of relationship between rates in open water and rates in bottles is evident in comparisons 2 and 3. It will be seen in Fig. 3 that the line of regression is notably displaced to the left of the origin, indicating that the rate of disappearance of inorganic phosphate from the open water is greater, by a nearly constant amount, than the rate of its decrease in the light bottle. An analogous relationship is evident in the third comparison (Fig. 4): The rate of decrease of inorganic phosphate in the open water is consistently higher than the rate

by which assimilation exceeds regeneration in the bottles. The asymmetric relationship in each of these comparisons is readily explained when one recalls that, with the exception of Tank 4, a layer of attached algae was allowed to accumulate on the tank walls. The demands which these plants made for dissolved phosphate account

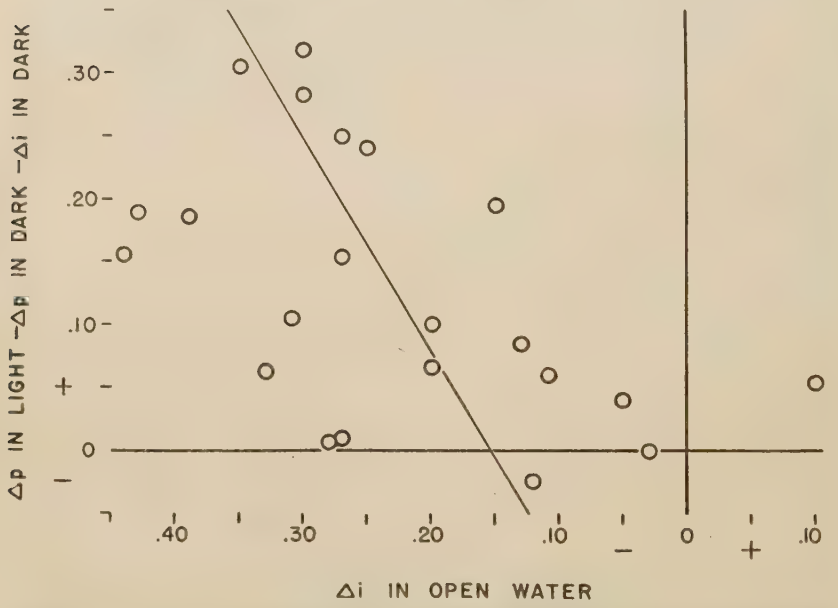

Figure 4. Correlation between the rate of change of inorganic phosphate concentration in the open water and the rate by which phosphorus assimilation exceeds regeneration in the bottles, in μg-at./L/day.

for the higher rate of phosphate disappearance in the open water than in the clean bottles (Fig. 3), and for the related anomaly in Fig. 4. In general, the data from Tank 4 do not show an excess loss of inorganic phosphate in the open water comparable to that in the other tanks.

We can conclude that, in spite of certain limitations, the dark and light bottle technique provides estimates of the rates of phosphorus assimilation, solution and regeneration which are highly consistent *inter se.* Moreover, such changes in phosphorus concentrations as could be measured in the surrounding water are significantly correlated with those in the bottles, indicating that the rates of phosphorus transformation measured within the bottles are representative of those prevailing in the larger environment.

RELATION BETWEEN PHOSPHORUS METABOLISM AND THE STANDING CROP AND GROWTH OF PHYTOPLANKTON

During the four weeks of measurement, the rates of the phosphorus transformations varied, as to be expected, with varying concentrations of phytoplankton and dissolved nutrients in the tank water. The highest recorded values for each of the three rates in the phosphorus cycle were as follows: assimilation (step 1) as measured by Δp in light $-$ Δp in dark $= 0.33$ μg-at./L/day; assimilation (step 1) as measured by Δi in dark $-$ Δi in light $= 0.36$ μg-at./L/day; solution (step 2) $=$ 0.38 μg-at./L/day; regeneration (step 3) $= 0.13$ μg-at./L/day. Due to errors in measurement or limitations in the bottle technique, negative values for assimilation, solution and regeneration occasionally appear in the data. These are theoretically impossible, of course, and should not be interpreted literally.

During the period of phosphorus measurements, the mean and maximum of observed chlorophyll concentrations were approximately 10.4 and 25.2 mg. chlorophyll a/m^3, respectively. In order that these values may be compared with concentrations observed in natural salt waters, data published by Riley are listed in Table I. The Long Island Sound and Georges Bank measurements cover all seasons of the year; those for the Tortugas are midsummer values.

TABLE I.—Chlorophyll Concentrations in Surface Waters

Locality	*Mg. chlorophyll/m³*		*Source*
	mean	*max.*	
Long Island Sound	17.44	62.00	Riley, 1941a
Georges Bank	5.58	27.20	Riley, 1941b
Tortugas region	0.33	0.47	Riley, 1938

In view of the importance of phosphorus in the growth and maintenance of the phytoplankton, the rates at which this element is taken up by living plant populations and released into solution by dead or dying cells, and perhaps even the rate of its regeneration to inorganic form, may be expected to show consistent relationships with the size and rate of increase or decrease of the phytoplankton population.

Correlation coefficients describing these relations are presented in Table II. The standing crop is measured as the arithmetic mean of the chlorophyll concentration in the open water at the beginning and at the end of the experiment, while the rate of population change is expressed as the increment (or decrement), per day, of the chlorophyll concentration during the experiment. Chlorophyll data are available for all

experiments with the exception of those running between August 11 and 13, giving a total of 18 complete sets of data. For this number, the values of the correlation coefficient for the 1%, 2% and 5% levels of significance are, respectively, .5897, .5425 and .4683.

TABLE II.—Correlation Coefficients for Rates of Phosphorus Assimilation, Solution and Regeneration versus Mean Chlorophyll Concentration and Rate of Change of Chlorophyll Concentration

	Mean chlorophyll	*Rate of change of chlorophyll*
Assimilation rate (Δp in light $-$ Δp in dark)	.555	.658
Assimilation rate (Δi in dark $-$ Δi in light)	.438	.598
Solution rate ($-$ Δp in dark)	.868	.038
Regeneration rate (Δi in dark)	.551	.176

Assimilation. The correlation of rate of phosphate uptake (step 1 in the cycle) with the phytoplankton standing crop differs considerably, depending upon which index of assimilation is used. Employing the measurement believed to be the more reliable, namely the changes

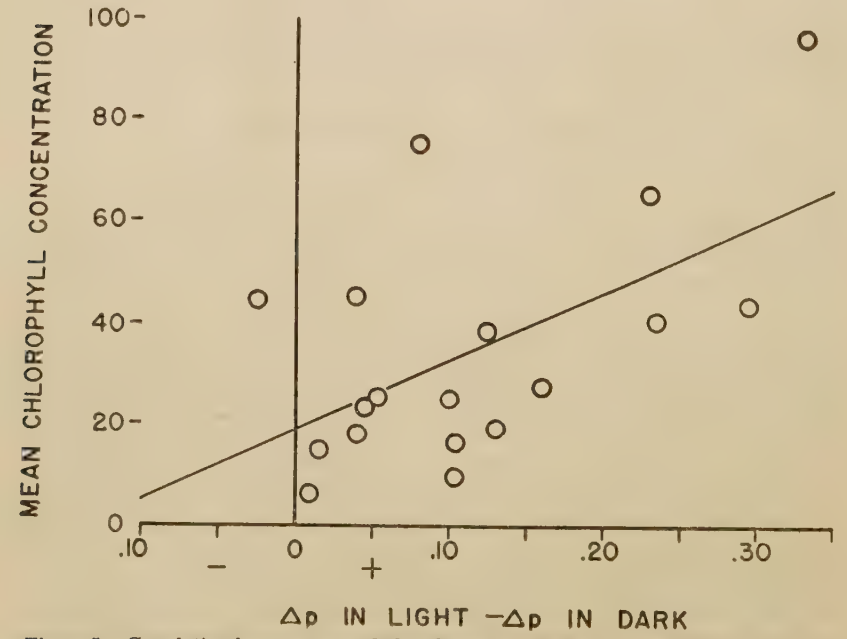

Figure 5. Correlation between rate of phosphorus assimilation in μg-at./L/day and mean concentration of chlorophyll *a* in Klett units/m³ (see text).

in particulate phosphorus (Fig. 5), the correlation is significant to the 2% level. Since it is to be expected on theoretical grounds that, in general, the larger the population the greater will be its demands for phosphate, the rather high correlation probably indicates a causal connection.

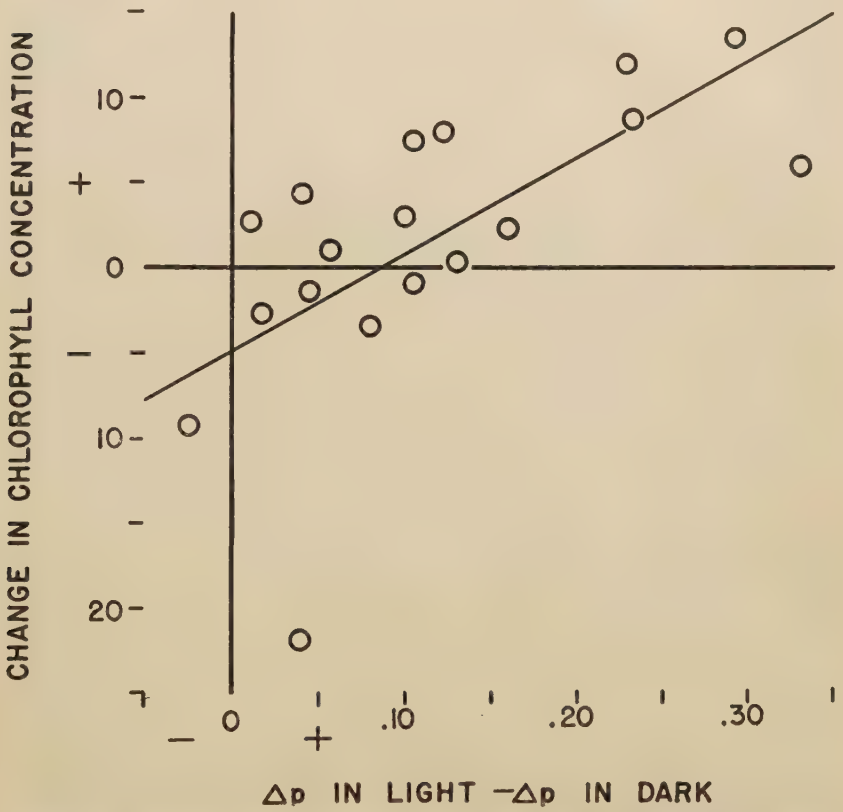

Figure 6. Correlation between rate of phosphorus assimilation (as measured by change in particulate phosphorus) in μg-at./L/day, and change in concentration of chlorophyll *a* in Klett units/m³/day (see text).

The rate of phosphorus assimilation shows a still stronger correlation with the growth rate of the phytoplankton (Figs. 6 and 7). By either measure of assimilation the correlation is significant to the 1% level. This again can be interpreted on biological grounds. A certain rate of phosphorus uptake is required for mere maintenance of the phytoplankton at a constant population density; the demands of

a growing population are considerably greater. However, if we can attach biological significance to the fact that the assimilation rate is more strongly correlated with population growth than with population size, an interesting deduction emerges from this comparison of the correlations. Provided we can assume that most or all of the phos-

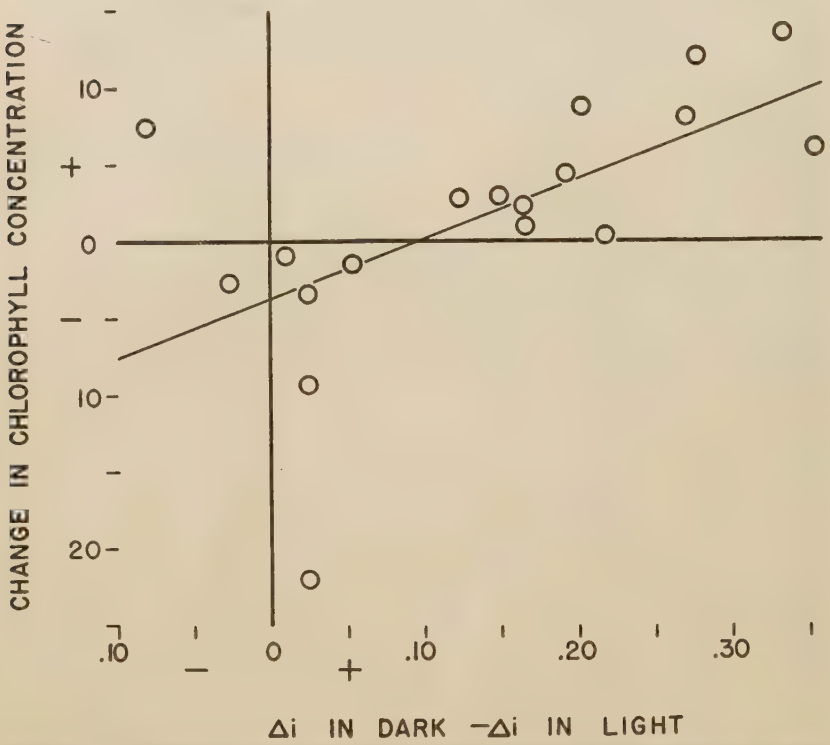

Figure 7. Correlation between rate of phosphorus assimilation (as measured by changes in inorganic phosphate) in μg-at./L/day, and change in concentration of chlorophyll *a* in Klett units/m³/day (see text).

phorus taken up is used in the synthesis of new organic matter through cell division (rather than in a metabolism of individual cells, absorbing and secreting phosphate, as postulated by Newcombe, 1940), the rate of phosphorus assimilation is a function of the rate of cell division. If this is true, the higher correlation of assimilation rate with population growth rather than with population size means that changes in population size were governed largely by changes in the rate of cell division rather than by changes in the death rate. That changes in

the division rate formed the principal mechanism of fluctuation in the standing crop is undoubtedly related to the fact that most of the population changes were increases. (Note that the single point in Figs. 6 and 7 representing a rapidly declining population quite visibly weakens the correlations.) However, there is no logical necessity relating the mechanism of change to the proponderance of increases; neither of these phenomena could have been predicted *a priori* from the other. Theoretically a population can increase by lowering the death rate, the "birth rate" remaining constant.

While the rate of phosphorus uptake is determined by both the size and the rate of increase of the population, it might be reasonably expected to depend also upon the concentration of phosphate available for assimilation. Ketchum (1939b) has shown a direct relation between the phosphate content of culture media and the rate of phosphorus absorption by *Nitzschia*. However, the correlation of assimilation rate with phosphate concentration in the tanks (not figured) falls a little short of the 5% level of significance, even when such factors as the presence or absence of added nitrate and the abundance of phytoplankton are taken into account by excluding experiments in which added nitrate was lacking and by plotting assimilation rate as the rate per unit of chlorophyll. If the rate of phosphorus uptake was significantly influenced by the phosphate content of the tank water, this relationship was partially obscured by other factors that were not measured.

Solution. The rate at which phosphorus is released into solution through the death and breakdown of cells (step 2 in the cycle) is closely correlated with the mean standing crop (Fig. 8), and there is every reason to believe that these variables are causally related.

The solution rate shows no significent relationship with the rate of population change. Here one might have expected to find a high negative correlation, but a moment's reflection will show that such a correlation would derive its principal strength from rapidly declining populations, which were almost entirely lacking in these experiments. In other words, while one tends to associate rapid decrease of particulate phosphorus with rapid decline of phytoplankton, there are no grounds for supposing that slowly *increasing* populations lose particulate phorphorus faster than rapidly increasing populations. There is, then, no reason to anticipate a strong negative correlation where population increases predominate, as in the present data.

Regeneration. It is clear from Fig. 9 that the relation between the rate of regeneration (step 3) and mean chlorophyll concentration could be described more accurately by a nonlinear equation. How-

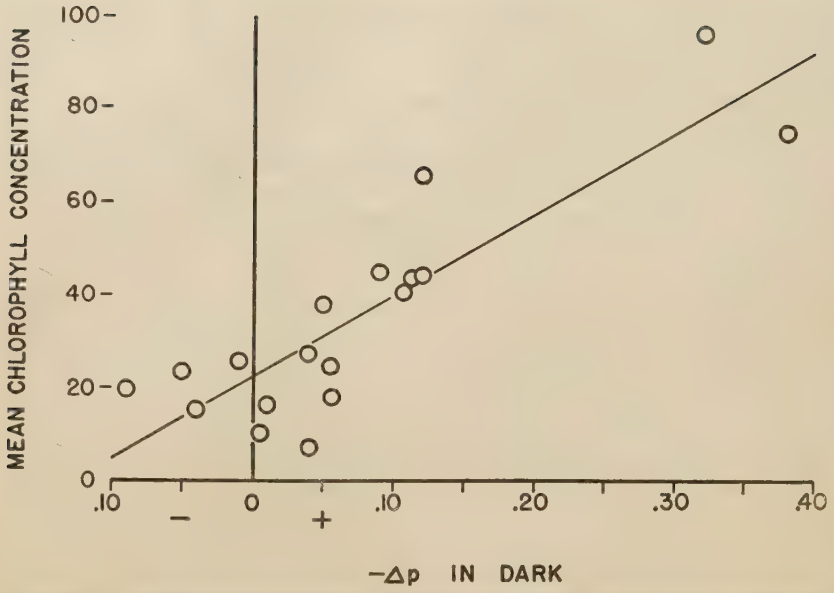

Figure 8. Correlation between rate of phosphorus solution in μg-at./L/day and mean concentration of chlorophyll *a* in Klett units/m³ (see text).

ever, even the somewhat inadequate straight line equation gives a correlation significant to the 2% level. In a general way, the larger the population the more rapidly is inorganic phosphate regenerated. Two factors appear to be operating here. As we have seen above, the rate of disintegration of particulate phosphorus is intimately related to the population size, and it may be that the dissolved organic products of that breakdown are almost instantaneously converted to inorganic form. Aside from this possible direct effect of population size upon regeneration rate, a secondary effect seems likely. The bacterial activity responsible for the regeneration of inorganic phosphate is doubtless a function of the surface area available to the bacteria, and this in turn is related to the abundance of phytoplankton (cf. ZoBell, 1946). It seems unlikely that all of the organic phosphorus released from the particulate phase reappears instantly as inorganic phosphate. Probably some or most of it is regenerated only after a lag of unknown duration in which the decomposing phosphorus compounds are present in dissolved organic form. In an attempt to detect such a lag, the regeneration rate as measured in each experiment was plotted against the mean chlorophyll value of the preceding two- or three-day period. However, simple inspection of the plot (not

figured) shows a correlation lower than that between regeneration rate and mean chlorophyll of the same experimental period. Evidently the peak of regeneration (if there is one at all) occurs either simultaneously with the decomposition of particulate phosphorus or more than two or three days later.

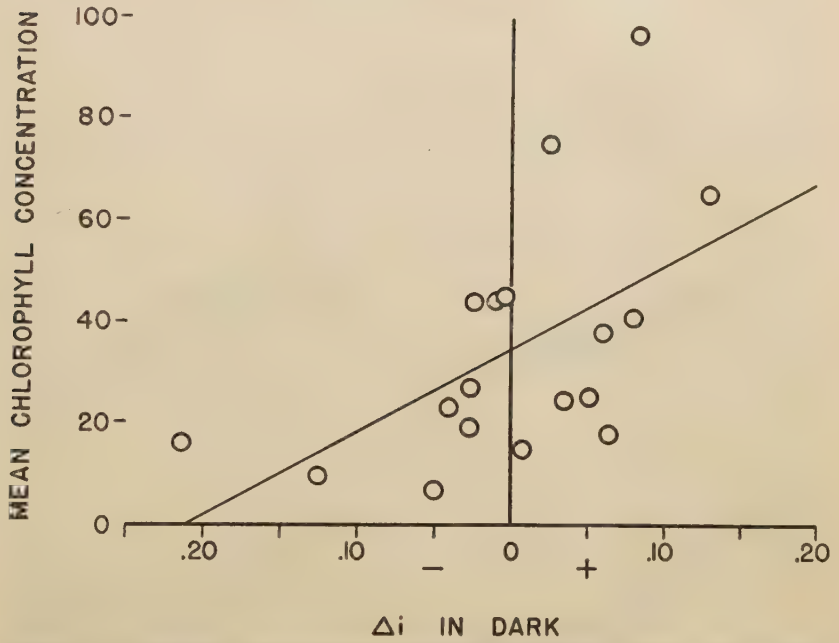

Figure 9. Correlation between rate of phosphorus regeneration in μg-at./L/day and mean concentration of chlorophyll *a* in Klett units/m³ (see text).

The regeneration rate shows no significant relation to the rate of population growth or decline.

Since regeneration is the process linking the two dissolved phosphorus fractions and is only remotely related to the particulate, it is to be expected that the rate of regeneration be more closely correlated with the concentration of dissolved organic phosphorus than with the particulate phase in the cycle. Unfortunately, dissolved organic phosphorus can be measured only as the difference between total phosphorus and the sum of the particulate and inorganic. As stated earlier, the measurement of total phosphorus frequently gave readings which were less than the sum of the inorganic and particulate fractions, resulting in "negative" values for the dissolved organic component.

A correlation of regeneration rate with the concentration of dissolved organic phosphorus as measured would thus be meaningless.

In summary, both the standing crop and the rate of change of the population determine its demands for phosphorus; whereas, in populations such as those studied, the rates of return of phosphorus to solution and to inorganic form depend upon the standing crop and are not affected by the rate of change of the population.

PHOSPHORUS CHANGES IN THE OPEN TANK WATER

One of the original objectives of this investigation was to draw up a balance sheet in which all of the changes in the various phosphorus fractions in the water-phytoplankton system could be accounted for.

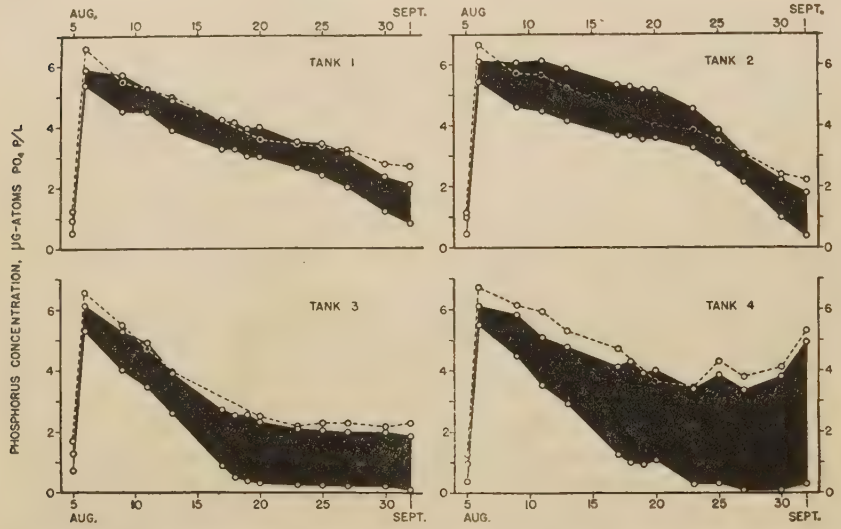

Figure 10. Concentrations of inorganic, particulate and "total" phosphorus in the open water of the tanks, August 5–September 1. Black area = particulate organic phosphorus; white area beneath black area = inorganic phosphate; total area beneath dashed line = "total" phosphorus (see text).

How imperfectly this aim was realized, except in Tank 4, can be seen immediately in Fig. 10 and Table III, which show the changes in the particulate and organic fractions and in the "total" phosphorus of the tank water over the entire period of observation. The concentration of inorganic phosphate dropped from initial values of more than 5 µg-at./L on August 6 to less than 1 µg-at./L on September 1. In three of the tanks, the increase of particulate phosphorus during the same interval was less than 1 µg-at./L. Thus the rapid disappearance

of inorganic phosphate was not balanced by a commensurate increase in particulate phosphorus. Nor, apparently, can it be accounted for by increase in the dissolved organic fraction, for measurements of total phosphorus, in so far as they are reliable, indicate losses amounting to as much as two-thirds of the phosphorus that was present in the water immediately after fertilizing.

TABLE III.—Phosphorus Changes in the Open Water of the Tanks, August 6–September 1

Tank	*Inorganic* μg-at./L	*Particulate* μg-at./L	*Loss of "total" phosphorus in* %
1	−4.57	+0.73	60
2	−5.14	+0.80	67
3	−5.22	+0.94	66
4	−5.22	+4.07	21

With respect to over-all changes in particulate and total phosphorus, the contrast between Tank 4 and the other tanks is conspicuous and instructive. Daily scraping of the sides and bottom of Tank 4 minimized the growth of attached algae, which in the remaining tanks produced a perceptible mat. The much greater loss of total phosphorus in the water of the first three tanks than in Tank 4 doubtless represents the demands of these fixed algae for dissolved phosphate. While the over-all decrease of inorganic phosphate was substantially the same in all tanks, by the end of the month a much greater proportion of this phosphorus was present in particulate form in Tank 4 than in the others. During the last two weeks of August, the water of Tank 4 supported a consistently denser phytoplankton population (by cell count) than did the other tanks, but it also contained considerably more detritus, as judged by gross inspection. The extent to which detritus contributed to the readings of particulate phosphorus cannot be estimated. It is quite clear, however, that scraping the tank walls profoundly affected the final distribution of phosphorus with the result that when observations were discontinued, four-fifths of the phosphorus originally present was accounted for by direct measurement. In contrast, where attached algae were allowed to grow undisturbed, they competed successfully with the plankton for the added phosphate, much of which was thus lost from the water.

Having added the benthic algae to our water-phytoplankton system, we can regard the momentary concentration of phosphorus locked up in this third component as resulting from the excess of uptake over release of phosphorus by these algae. Evidently these processes struck an equilibrium in Tank 3 on about August 20; thereafter the

return of phosphorus to the water just balanced its removal by the attached algae, and the concentration of total phosphorus in the water remained nearly constant at 2.2 μg-at./L. In Tank 4, where attached algae played a less important role, this equilibrium was poised at about 3.8 μg-at./L. (There is reason to believe that the apparent fluctuations about this value and the indicated increase in total phosphorus at the end of the period may have been due to varying degrees of thoroughness in scraping and stirring Tank 4, rather than to biological changes.) In the water of Tanks 1 and 2, total phosphorus did not reach a constant value and was still decreasing at the end of the investigation.

Finally, Fig. 10 illustrates the fact demonstrated by Ketchum (1939b) with *Nitzschia* cultures that the rate of phosphate assimilation depends upon the nitrate content of the medium. In Tanks 3 and 4, which were fertilized with nitrate as well as phosphate, the inorganic phosphate concentration dropped at a steady pace from August 6 to 18. Using the same interval for comparison with the tanks initially fertilized with phosphorus alone, we find the following rates of decrease in inorganic phosphate per day; Tank 1, 0.18; Tank 2, 0.15; Tank 3, 0.40; Tank 4, 0.38 μg-at./L. Following the addition of nitrate to Tanks 1 and 2 on August 20, the rate of phosphate depletion from the water in Tank 2 was exactly doubled. For unknown reasons, in Tank 1 the rate of phosphorus assimilation was not appreciably accelerated by the addition of nitrate.

DISCUSSION

In fresh or salt water ponds and in the sea, one may frequently observe dense phytoplankton blooms associated with extreme dilutions of inorganic phosphate. At first glance this may appear paradoxical, in view of the well established importance of phosphate to plant growth. However, consideration of the dynamic aspects of phytoplankton nutritution prevents one from falling into the error of concluding from this observation that phosphate is not an important nutrient. The essential factors are the rate of assimilation of phosphate and the rate of its replenishment.

Thus it becomes a matter of great theoretical interest to know the actual rates at which phosphorus passes from one form to the next in its cycle, and how these rates are related to the abundance of phytoplankton, its increase or decrease, and to the concentration of inorganic phosphate in the water. In the experiments described, it was shown that assimilation rate depends more upon the rate of population increase than upon its absolute size. Thus the phosphorus requirements of a large population which is not increasing its mass may be

satisfied by a relatively low rate of assimilation. It was also found that the quantity of phosphorus assimilated per day can be as great as the momentary concentration of inorganic phosphate in the water; in one experiment a dense population (approximately 19.6 mg. chlorophyll *a*/m³) removed .08 μg-at. P/L per day from water in which the phosphate concentration was .08 μg-at./L at the beginning and at the end of the experiment. This makes it appear probable that in natural situations where phytoplankton blooms are associated with low concentrations of inorganic phosphate, the time required for the complete replacement of that phosphate may be only a matter of hours.

The rate of regeneration as measured was consistently lower than the rates of assimilation and solution. Probably part of this difference is due to the incomplete measurement of regeneration, but in so far as the comparison is real it indicates that the rate of regeneration limits the velocity of the entire phosphorus cycle. This conclusion has an important bearing on the problem of organic production in the sea, for wherever phosphate is present in concentrations low enough to limit plant growth, the rate of its replenishment will determine the rate at which it can be assimilated. On the basis of phosphorus measurements in the surface waters of the Sargasso Sea, where the concentration of dissolved organic is rather high, the particulate low and the inorganic almost negligible, B. H. Ketchum (in litt.) has advanced the opinion that the rate of phosphorus regeneration may limit the rate of production of organic matter. His view is supported by the present data.

Since zooplankton organisms excrete inorganic phosphate (Gardiner, 1937) derived from the phytoplankton (and detritus) upon which they subsist, it is possible that they play an important role in the phosphorus cycle. However, until suitable measurements are made to investigate this problem, the effect of the zooplankton upon the circulation of phosphorus must remain a matter of conjecture.

A knowledge of phosphorus metabolism rates is essential to the most efficient management of a program of fertilizing natural waters. In published reports dealing with the fertilization of natural waters, one frequently finds the assumption that phosphorus assimilated by the phytoplankton can be equated with the disappearance of added phosphate from the water. The folly of this supposition can be illustrated from the present data. The concentration of inorganic phosphate immediately following fertilization was more than 5 μg-at./L. If attached algae were allowed to grow on the tank sides and bottom, by the end of the month only 23 to 32% of this initial phosphate endowment was present in the plankton; 73 to 82% had found its way into the attached flora. Moreover, in natural bodies of

water, even in the absence of any fixed vegetation competing for nutrients with the plankton, an important part of the added phosphate is apt to be adsorbed, at least temporarily, on colloidal bottom deposits (Ohle, 1937; Einsele, 1938; Hutchinson, 1941; Mortimer, 1941). In the well weathered concrete tanks this loss of phosphorus from the water-phytoplankton system was reduced to a minimum. Even so, the escape of phosphorus from the open water to attached vegetation was so rapid as to render impossible any estimate of phosphorus utilization by the plankton, from rates of phosphate depletion alone. Thus it has been shown that the actual assimilation by the phytoplankton can be determined only by direct measurement of the phosphorus taken into the plant cells.

SUMMARY

1. By the use of the "dark and light bottle" method in outdoor concrete tanks, measurements have been made of the rates at which phosphorus is regenerated, assimilated, and released into solution in fertilized salt water and its contained phytoplankton. The maximum recorded rates were: regeneration = 0.13 μg-at./L of sea water in the tanks/day; assimilation = 0.36 μg-at./L/day; solution = 0.38 μg-at./L/day. The highest observed assimilation rate was measured in water containing approximately 20 million cells/L and 25 mg. chlorophyll a/m^3.

2. In 18 series of measurements, during which phytoplankton increases predominated over decreases, the following relations were observed between the rates of phosphorus transformations and the size and absolute change of size of the phytoplankton populations:

a. The rate of phosphorus assimilation was significantly correlated with the size of the phytoplankton standing crop and showed an even stronger dependence upon the increment of growth.

b. The rate at which particulate organic phosphorus was released into solution from dead plankton organisms was intimately related to the size of the standing crop and was independent of the change in population size (which in most cases was an increase).

c. The regeneration of dissolved inorganic phosphate from dissolved organic phosphorus depended upon the phytoplankton standing crop and showed no relation to the change in population size.

3. If attached algae were allowed to grow on the sides and bottom of the tanks, in less than one month they removed three-fourths of the added phosphate from the water-phytoplankton system. Where attached algae were largely prevented from growing, four-fifths of the phosphorus originally present was detected in the water at the end of four weeks.

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